European Society for Evolutionary Biology

ABSTRACTS

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The evolution of spite

ENDLESS FLIES MOST BEAUTIFUL : THE ROLE OF CIS-REGULATORY DNA SEQUENCES IN THE ORIGIN OF MORPHOLOGICAL NOVELTY AND DIVERSITY

Sean B. Carroll [1]

[1] *HHMI, University of Wisconsin, 1525 linden Dr., 53706, Madison, USA*

sbcarrol@wisc.edu

One of the general issues concerning the evolution of form is the relative contribution of gene duplication, protein sequence evolution, and regulatory sequence evolution to the generation of morphological variation and diversity. We have analyzed the gain, loss , and modification of pigmentation patterns in Drosophila as models of morphological evolution. Eight cases have involved regulatory changes at pleiotropic pigmentation genes. These include the surprising independent gains of similar wing patterns via the co-option of distinct cis-regulatory elements and the gain and loss of abdominal patterns via the gain and loss of Hox binding sites. Our results demonstrate how the functional diversification of the modular cis-regulatory elements of pleiotropic genes contributes to evolutionary novelty and the independent evolution of morphological similarities.

EVOLUTION IN THE TROPICS: DOBZHANSKY REVISITED

Douglas W. Schemske [1]

[1] *Michigan State University, Plant Biology, 166 Plant Biology, 48824, East Lansing, USA*

schem@msu.edu

One of the major unresolved questions in biology concerns the factors responsible for the extraordinary diversity of tropical regions. While numerous studies have investigated the ecological processes that contribute to high tropical diversity, few have addressed its origins. Dobzhansky's "Evolution in the Tropics" (American Scientist. 1950. 38:209-221) remains the most influential contribution, but he provided few specifics in support of his hypothesis that the greater importance of biotic interactions in the tropics was the cause of latitudinal diversity gradients. I will briefly review the evidence and traditional explanations for high tropical diversity, then discuss a new evolutionary hypothesis regarding the role of biotic interactions. The central premise is that geographic differences in the importance of biotic factors will influence the opportunity for coevolution, and hence rates of divergence. In the tropics, strong biotic interactions and spatial variation in community composition promote coevolution, and as a result, the optimal phenotype is a “moving target”. In contrast, evolutionary divergence in temperate populations is governed primarily by spatial differences in abiotic factors, which do not coevolve; hence, the optimum phenotype represents a “fixed target”. Thus, adaptation and speciation in tropical environments are expected to proceed faster than in temperate regions.

THE PEPPERED MOTH: THE PROOF OF DARWINIAN EVOLUTION

Michael E. N. Majerus [1]

[1] *University of Cambridge, Department of Genetics, Downing Street, Cambridge, CB2 3EH, UK*

mike.majerus@gen.cam.ac.uk

The evolution of melanism in the peppered moth, following the industrial revolution in Britain, is the most cited example of an observed heritable change that resulted from Darwinian evolution. The reason for this is that the change was visually obvious, was observed, and could be explained by Darwin's central mechanism of evolution – natural selection. Further, the reason that the black form was fitter than the pale form was easy to understand: against lichen denuded and smoke blackened bark, the black moths were better camouflaged, and so were less often found and eaten by birds.

Over the last few years, creationists have seized upon design flaws in Bernard Kettlewell's classical experiments in the 1950s. They claim that these flaws, and more recent allegations of fraud aimed at Kettlewell and a conspiracy of silence among evolutionary biologists, particularly in Britain, fatally undermine this cornerstone of Darwinian evolution, and therefore the basic theory of evolution by natural selection. Most biologists who have worked on the peppered moth take the view that although Kettlewell's experiments did contain design flaws, these flaws would only have affected the quantitative accuracy of his tests; not the qualitative interpretation that differential bird predation has played a major role in the evolution of melanism in the peppered moth.

The question I will address is whether melanism in the peppered moth should still be regarded as an example, par excellence, of Darwinian evolution in action. I will consider the validity of criticisms of the peppered moth case, and briefly describe results of new experiments to test whether differential bird predation is the main agent of selection that led to the rise and fall of the melanic peppered moth.

THE EVOLUTIONARY ENIGMA OF SEX

Sarah P. Otto [1]

[1] *University of British Columbia, Department of Zoology, 6270 University Blvd., Vancouver BC V6T 1Z4, Canada*

otto@zoology.ubc.ca

One of the greatest puzzles in evolutionary biology is the high frequency of sexual reproduction and recombination. Given that individuals surviving to reproductive age have genomes that function in the current environment, why should they risk shuffling their genes with those of another individual? Mathematical models are especially important in developing predictions about when sex and recombination can evolve, because it is difficult to intuit the outcome of evolution with several interacting genes. Interestingly, theoretical analyses have shown that it is often quite difficult to identify conditions that favour the evolution of high rates of recombination. One reason why an answer to the paradox of sex has been so elusive is that our models have focused unduly on populations that are infinite in size, unstructured, and isolated from other species. Yet most verbal theories for sex and recombination consider a finite number of genotypes evolving in a biologically and/or physically complex world. In this talk, I review the various hypotheses for why sex and recombination is so prevalent and discuss theoretical results indicating which of these hypotheses is most promising. I also discuss how evolutionary forces act on the timing of sexual reproduction and on covariation between fitness and mode of reproduction.

NAVIGATING THE FOREST OF GENE TREES, FROM PHYLOGEOGRAPHY TO PHYLOGENOMICS

Scott V. Edwards [1]

[1] *Harvard University, Department of Organismic and Evolutionary Biology, 26 Oxford Street, Cambridge, MA 02138, USA*

sedwards@fas.harvard.edu

At both the population- and higher taxon-levels, single locus analyses of molecular variation are giving way to multilocus analyses involving tens if not hundreds of coding and noncoding regions of the nuclear genome. In phylogeographic studies, for example, anonymous DNA sequence regions of the nuclear genome have the advantage over microsatellites of being amenable to phylogenetic analysis. Despite these advantages, the distinction between gene trees, species trees, and diverse processes operating at the level of populations and species, are not always clear. In this talk I will review the critical distinction between gene trees and species trees and suggest that, although the latter is of primary interest in phylogenetics and phylogeography, phylogenetic analyses almost invariably estimate the former, primarily because methods for estimating the latter have only recently become accessible. Using multilocus data sets at several levels of divergence, I will show that an explicit focus on the species trees provides a measure of coherence to an often bewildering array of discordant gene trees. I will discuss a novel and efficient Bayesian approach to estimating phylogenetic trees (Liu and Pearl, *Syst. Biol*, 2007.) that focuses, appropriately, on species, rather than genes, and which is applicable to all times scales and data sets, regardless of degrees of discordance among genes due to incomplete lineage sorting. Like other recent methods for estimating population parameters from multilocus data, the species tree approach is naturally more complex than traditional phylogenetic approaches, if only because it acknowledges an additional level of organization, the species, above the level of genes and gene trees. Nonetheless, it provides a compelling new way to combine data in phylogeographic and phylogenomic studies that focuses attention on the singularity of species histories, and away from the heterogeneity frequently found at the level of individual genes.

HOW ESEB WAS FOUNDED AND HOW IT GREW

Stephen C. Stearns [1]

[1] *Yale University, Ecology and Evolutionary Biology, P.O. Box 208102, 06520, New Haven, CT, USA*

stephen.stearns@yale.edu

ESEB grew out of an earlier, less formal organization. It was catalyzed by the desire to have a journal and by a publisher's offer to produce that journal, but only if there were a society to back it up. My experiences at a conference in Denmark in the summer of 1985 stimulated me to try to found the society; my efforts would have gone nowhere had they not met with broad support. The founding conference in Basel in 1987 was a big success, with much greater attendance than we had anticipated; since then attendance has grown steadily, with some fluctuations, to an impressive plateau. There were three key events in the growth of the journal. First, Birkhaeuser undertook the financial risk of starting it and promoting it, a decision for which we must thank Hans-Peter Thur. Second, when it became evident that Birkhaeuser did not have the best access to the critical markets, ESEB decided to entertain bids for the journal, and chose Blackwells. That choice has had important positive impact on the Society's finances and thus its ability to support conferences and other activities. Third, under Rolf Hoekstra the journal moved to a system of rapid review. Rapid reviews and Blackwells' reputation and advertising combined with the quality of the articles published to lift the journal into the top ranks in its field. That is a brief outline of the history of the society and its journal. I intend to enliven it with anecdotes, any photographs that I can lay my hands on, and any brief summary statistics I can assemble.

THE EVOLUTION OF SPITE

Andy Gardner [1]

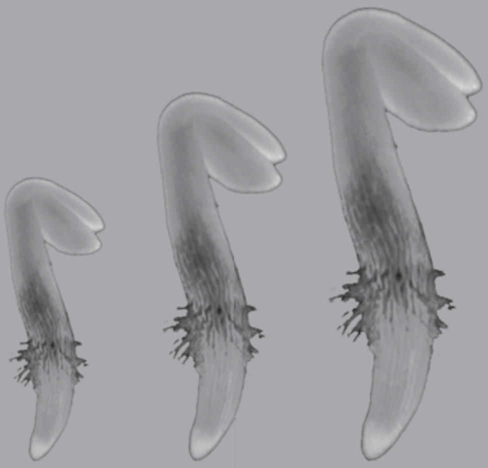
[1] *Edinburgh University, Institute of Evolutionary Biology, Edinburgh, UK*

andy.gardner@sjc.ox.ac.uk

Spite, altruism’s neglected ugly sister, is the most mysterious and controversial of the four social behaviours. How can an individual be favoured to harm itself and its social partners? Hamilton’s rule, which was devised in order to explain altruistic behaviours, has a darker side that reveals when spite will be favoured. Specifically, it requires that the spiteful actor and its victims be negatively related. I develop theory for the evolution of spite in competitive environments, and show that increasingly strong local competition can favour spiteful behaviour. Application of the theory to chemical warfare in microbes and suicidal sibling rivalry in parasitoid wasps leads to novel predictions for parasite virulence and sex allocation theory. I discuss the semantics of spite and ambiguities in the standard classification of social behaviours.

1

Evolutionary genetics of coloration



Program

Tuesday August 21 *Location:* Ekonomikum 3

Symposium 1: Evolutionary genetics of coloration

ORGANIZERS: Nick Mundy, University of Cambridge, UK
Patricia Beldade, Leiden University, The Netherlands

09.45-10.15	**Nicolas Gompel** (invited) Repeated morphological evolution by cis-regulatory changes
10.15-10.45	**David Parichy** (invited) Evolutionary genetics of zebrafish pigment pattern development
10.45-11.05	**Hopi Hoekstra** The production of adaptive colour pattern by interacting genes
11.05-11.35	*Coffee*
11.35-11.55	**Jake Gratten** Cryptic selection on coat colour in Soay sheep
11.55-12.15	**Walter Salzburger** The (adaptive) evolution of colour genes in cichlid fishes
12.15-12.35	**Arielle Cooley** Genetic analysis of floral colour patterning in Chilean Mimulus
12.35-14.00	*Lunch*
14.00-14.20	**Patricia Wittkopp** Genetic basis of pigmentation differences within and between Drosophila species
14.20-14.40	**Terry Burke** Convergent evolution of plumage polymorphisms in domestic birds: The lavender phenotype
14.40-15.00	**Pieternella Luttikhuizen** Shell colour polymorphism: using the locus comparison approach to test for balancing selection in the Baltic tellin
15.00-15.20	**Jenny Boughman** Selective mechanisms and genetics of color divergence in threespine sticklebacks
15.20-16.00	Coffee

01-01 Talk

REPEATED MORPHOLOGICAL EVOLUTION BY CIS-REGULATORY CHANGES

Nicolas Gompel [1]

[1] *IBDML, CNRS UMR 6216, case 907, Parc scientifique de Luminy, 13288, Marseille cedex 9, France*

gompel@ibdml.univ-mrs.fr

The independent evolution of morphological similarities is widespread. Although the modification of morphological trait is generally associated with changes in gene regulation during development, the molecular mechanisms underlying parallel evolutionary changes have remained elusive. In particular, the extent to which the course of evolution is constrained to follow certain genetic paths is largely unknown. We addressed this question by studying the evolution of a male wing pigmentation spot involved in courtship display that has been gained and lost multiple times in a Drosophila clade. Each of the cases we have analyzed (two gains and two losses) involved regulatory changes at the pleiotropic pigmentation gene yellow. Losses involved the parallel inactivation of the same cis-regulatory element (CRE), while the independent gains of wing spots resulted from the co-option of distinct ancestral CREs. These elements have gained multiple binding sites for transcription factors that are deeply conserved components of the regulatory landscape controlling wing development. These results demonstrate how the functional diversification of the modular CREs of pleiotropic genes contributes to evolutionary novelty and the independent evolution of morphological similarities.

01-02 Talk

EVOLUTIONARY GENETICS OF ZEBRAFISH PIGMENT PATTERN DEVELOPMENT

David M. Parichy [1]

[1] *University of Washington, Department of Biology, 98195, Seattle, USA*

dparichy@u.washington.edu

Pigment patterns of Danio fishes are a tractable system for studying the evolution of developmental mechanisms and how these mechanisms influence patterns of phenotypic variation. Danios exhibit a diverse array of adult pigment patterns ranging from horizontal stripes in the zebrafish, D. rerio, to a uniform pattern in D. albolineatus, to vertical bars in D. choprae. Here, I report on recent progress in understanding the genetic and cellular bases for pigment pattern diverisification in this group, and how genetic approaches can be used to reveal homology and evolutionary novelty during pigment pattern development.

01-03 Talk

THE PRODUCTION OF ADAPTIVE COLOR PATTERN BY INTERACTING GENES

Hopi E. Hoekstra [1], Cynthia C. Steiner [1]

[1] *Harvard University, Department of Organismic and Evolutionary Biology and The Museum of Comparative Zoology, Cambridge, MA 02138, USA*

hoekstra@oeb.harvard.edu

Despite the fact that many groups of vertebrates share similar color patterns, we are largely ignorant of the developmental, genetic and molecular basis of this variation. In this talk I will discuss how we identified the genetic changes contributing to an adaptive difference in color pattern between two subspecies of mice (*Peromyscus polionotus*), in which one mainland subspecies has a cryptic dark brown dorsal coat, while a younger beach-dwelling subspecies has a lighter coat produced by natural selection for camouflage on pale coastal sand dunes. Using genome-wide linkage mapping, we identified three chromosomal regions associated with differences in pigment pattern, with most of the pigmentation difference due to two candidate genes *Agouti signaling protein* (*Agouti*) and *Mc1r*. These genes interact epistatically in a way that suggests that the derived *Agouti* allele must have been selected *before* the derived *Mc1r* allele. In this case, then, the underlying genetics suggests that this adaptive color pattern is due to just a few genes of large effect, and that the way they interact may tell us the order in which they evolved. The genetic basis of pigmentation in these mice provides clues to how adaptation proceeds at the molecular level in nature and may help explain color patterns in other vertebrates.

01-04 Talk

CRYPTIC SELECTION ON COAT COLOUR IN SOAY SHEEP

Jake Gratten [1], Alastair J. Wilson [2], Allan F. McRae [3], Dario Beraldi [2], Peter M. Visscher [3], Josephine M. Pemberton [2], Jon Slate [1]

[1] *The University of Sheffield, Animal and Plant Sciences, Western Bank, S102TN, Sheffield, UK*
[2] *University of Edinburgh, Institute of Evolutionary Biology, West Mains Road, EH93JT, Edinburgh, UK*
[3] *Queensland Institute of Medical Research, Genetic Epidemiology, 300 Herston Road, 4029, Brisbane, Australia*

j.gratten@sheffield.ac.uk

Integrating measures of individual fitness in natural populations with an understanding of the molecular basis of phenotypic variation is an enduring goal in evolutionary genetics, because such links promise to shed light on the role of selection in the maintenance of genetic variation. Here, we present a quantitative genetic analysis of selection on a stable coat colour polymorphism in a free-living population of Soay sheep. Colour in Soay sheep is either dark or light, depending on inheritance of a single recessive non-synonymous substitution in the *TYRP1* gene; dark sheep have genotype GG or GT and light sheep are TT homozygotes. Previous work has revealed that dark sheep are larger than light sheep, and that there is directional selection for larger body size. This raises the question of how variation for coat colour is maintained. In this study we used animal models to quantify the genetic association between coat colour, body size and fitness. We found evidence for genetic association and linkage between *TYRP1* and both birth weight and fitness. However, whereas both genotypic classes of dark sheep (GG and GT) were larger than light sheep (TT), homozygous dark sheep (GG) had significantly lower fitness than both light sheep (TT) and dark heterozygotes (GT). At a phenotypic level there was no evidence for selection on coat colour. These findings suggest that *TYRP1*, or tightly linked QTL, influence fitness via two distinct mechanisms, one 'direct' but cryptic, and a second via effects on body size. The total selection on *TYRP1* favours the T allele, because the direct positive effects of T on fitness outweigh the negative effects associated with smaller body size. We show that consistent with expectations based on relative fitness, the frequency of allele T has increased in the last twenty years.

01-05 Talk

THE (ADAPTIVE) EVOLUTION OF COLOR GENES IN CICHLID FISHES

Walter Salzburger [1, 2, 3], Ingo Braasch [3, 4], Axel Meyer [3]

[1] *University of Lausanne, Department of Ecology and Evolution, Le Biophore, 1015, Lausanne, Switzerland*
[2] *University of Basel, Department of Environmental Sciences, Vesalgasse 1, 4051, Basel, Switzerland*
[3] *University of Konstanz, Department of Biology, Universitaetsstrasse 10, 78457, Konstanz, Germany*
[4] *University of Wuerzburg, Physiological Chemistry I, Am Hubland, 79074, Wuerzburg, Germany*

walter.salzburger@unil.ch

The exceptionally diverse species flocks of cichlid fishes in the East African Great Lakes are prominent examples for replicate adaptive radiations and explosive speciation. The hundreds of closely related cichlid species differ greatly in ecologically relevant traits such as mouth morphology and dentition. Cichlids also display a great diversity in coloration and pigmentation patterns indicating the importance of sexual selection in this group. We have studied the molecular evolution of nine candidate color genes in East African cichlid species and find evidence for adaptive sequence evolution in some of them. For example, we can show that csf1ra evolved under positive selection in the ancestor of the haplochromines (the most species-rich group of cichlids), in which this gene is expressed in the egg-dummies on male anal fins. These egg-spots mimic real eggs and play a crucial role in the breeding cycle of these mouth-brooding fish by guiding the female's mouth close to the male's genital opening. This facilitates the fertilization of the eggs within the female's mouth. The comparative analysis of color genes also provides novel insights into the general patterns of evolution in East African cichlids.

01-06 Talk

GENETIC ANALYSIS OF FLORAL COLOR PATTERNING IN CHILEAN MIMULUS

Arielle M. Cooley [1], John H. Willis [1]

[1] *Duke University, Biology Department, Box 90338, 27708, Durham, NC, U.S.A.*

acooley@gmail.com

The molecular basis of evolutionary change is most easily studied in traits whose underlying biosynthetic pathways are well understood. The anthocyanin pigment pathway is relatively simple, comprised of known genes, and has often been implicated in flower color variation. Although much of this variation is due to loss-of-function mutations, work in some genera (Antirrhinum, Petunia) focuses on changes in the spatial distribution of pigment rather than its presence or absence. Analysis of color patterning in additional systems will help address general questions such as the relative importance of structural versus regulatory changes, and whether the same genes are involved repeatedly.

The emergence of Mimulus as a model system, with a fully-sequenced genome as well as a wide range of phenotypic and ecological diversity, makes it an excellent choice for such studies. I present a genetic analysis of floral color patterning in four closely related Mimulus species that show a dramatic, phylogenetically restricted diversification within a large and otherwise-homogeneous monophyletic group. Crosses reveal complex spatial patterning of a single anthocyanin pigment, cyanidin. All taxa are capable of producing cyanidin, indicating that changes are not due to loss-of-function mutations. Segregation in mapping populations suggests modularity, with several patterning elements behaving as simple Mendelian traits. I am using a combination of mapping and candidate gene approaches to identify the underlying genes. I have identified one transcription factor, the ortholog of ROSEA (Antirrhinum) and AN2 (Petunia), that shows complete association with one patterning element, and will present additional results this summer.

01-07 Talk

GENETIC BASIS OF PIGMENTATION DIFFERENCES WITHIN AND BETWEEN DROSOPHILA SPECIES

Patricia Wittkopp [1], Belinda Hareum [1], Emma Stewart [1], Adam Neidert [1], Gabriel Smith-Winberry [1]

[1] *University of Michigan, Ecology and Evolutionary Biology, 830 N. University Ave., 48109, Ann Arbor, MI, USA*

wittkopp@umich.edu

Discovering the genetic basis of phenotypic divergence is essential for understanding evolutionary mechanisms. New mutations and standing genetic variation both provide raw material for evolutionary change, but the relative contribution of each is largely unknown. To examine the source of variation used for interspecific divergence, we are studying pigmentation differences within and between Drosophila species in the virilis group. D. novamexicana is a young species that evolved yellow pigmentation since its divergence from D. americana approximately 380,000 years ago. D. americana has brown pigmentation that ranges from dark to light in an east to west cline and is consistent with local adaptation. Two genes, ebony and tan, have been identified that appear to contribute to pigmentation differences between species. These genes encode enzymes that catalyze opposite directions of a reversible reaction in the pigment biosynthesis pathway. Haplotypes of ebony and tan fixed in D. novamexicana are segregating in D. americana and contribute to pigmentation differences within this species, suggesting that standing genetic variation may be an important source of phenotypic divergence.

01-08 Talk

CONVERGENT EVOLUTION OF PLUMAGE POLYMORPHISMS IN DOMESTIC BIRDS: THE LAVENDER PHENOTYPE

Terry Burke [1], Mohsen Vaez [1], Sarah Johns [1], Michèle Tixier-Boichard [2]

[1] *University of Sheffield, Dept of Animal & Plant Sciences, S10 2TN, Sheffield, UK*
[2] *INRA/INA P-G, Centre de Recherches de Jouy, UMR Génétique et Diversité Animales, 78352, Jouy-en-Josas, France*

t.a.burke@sheffield.ac.uk

Few of the genes that determine variation in feather colour, feather pattern, or bodily distribution of colour and pattern have as yet been described. Many genes that affect pigmentation have been described in mice. We have investigated several of these mouse loci as candidates for variation in avian plumage and shown, in a segregation analysis, that mutations at one of these loci, melanophilin (MLPH), account for the lavender phenotype in the chicken. An apparently similar recessive dilution mutation is commonly maintained in several other domesticated and captive bird populations, including quail, muscovy duck, guineafowl, turkey, pigeon and Eurasian blackbird. In most of these cases we have shown that the same locus accounts for the phenotype, and in some but not all cases the same mutable CpG site accounts for the polymorphism. While the data in this field are as yet based on rather few loci, our results add to an emerging picture that much of the colour variation that occurs in vertebrates may be accounted for by a small homologous subset of the very many loci that might potentially be involved.

01-09 Talk

SHELL COLOUR POLYMORPHISM: USING THE LOCUS COMPARISON APPROACH TO TEST FOR BALANCING SELECTION IN THE BALTIC TELLIN

Pieternella C. Luttikhuizen [1]

[1] *Netherlands Institute for Sea Research, Marine Ecology and Evolution, P.O. Box 59, Den Burg, The Netherlands*

luttik@nioz.nl

Colour polymorphisms of molluscan shells have fascinated humans around the globe and throughout history. They are often considered to be maintained by balancing selection, e.g. due to apostatic selection; frequency dependent predation. Yet, neither genetic basis nor adaptive significance of these widespread polymorphisms are well understood. A common way to approach putative adaptive significance has been to experiment with hypothetical causal agents. An alternative is the 'locus comparison approach', which contrasts spatial differentiation of neutral molecular markers with that of other genes of interest. We use the locus comparison aproach to test for balancing selection in the bivalve mollusc *Macoma balthica* L., which is polymorphic for red, orange, yellow and white. On the basis of laboratory reared families we infer a model of inheritance for the colour polymorphism. Population differentiation for shell colour variation is then contrasted with molecular marker differentiation.

01-10 Talk

SELECTIVE MECHANISMS AND GENETICS OF COLOR DIVERGENCE IN THREESPINE STICKLEBACKS

Jenny W. Boughman [1], Eva J. Lewandowski [1], Catherine Peichel [2], Tiffany Malek [2]

[1] *University of Wisconsin-Madison, Zoology, 430 Lincoln Drive, 53706, Madison, WI, USA*
[2] *Fred Hutchinson Cancer Research Center, Human Biology, 1100 Fairview Ave N, 19024, Seattle, WA, USA*

jboughman@wisc.edu

To understand the evolution of male nuptial color in threespine sticklebacks we integrate work investigating how selection acts on color with studies elucidating its genetic basis. Populations differ in male color: in some populations males express red nuptial color while in others males express black. This divergence is the result of sensory drive. Populations in clear water express red nuptial color while those in red-shifted water express black color. Moreover, female perception of color correlates with water color and leads to differences in color preference. This alters sexual selection on male color and contributes to its divergent evolution. We explore the genetic basis of these color differences through a combination of quantitative genetics and QTL mapping. Our quantitative genetic study indicates that color differences arise through the combined effects of genetics and phenotypic plasticity. Our mapping work finds several QTL of moderate effect on three chromosomes, but no sex linkage. Finally, we have evidence suggesting that color and color perception may be genetically linked. Such linkage would facilitate the coevolution of color and color preference, and may help to explain their rapid divergent evolution.

01-01 Poster

COLOUR POLYMORPHISM AND POPULATION DIVERGENCE IN A PARROT RING SPECIES: A ROLE FOR SEXUAL SELECTION?

Mathew L. Berg [1], Raoul F. H. Ribot [1], Leo Joseph [2], Katherine L. Buchanan [3], Andrew T. D. Bennett [1]

[1] *University of Bristol, School of Biological Sciences, Woodland Road, BS8 1UG, Bristol, United Kingdom*
[2] *CSIRO, Australian National Wildlife Collection, Bellenden Street, 2911, Crace, Australia*
[3] *Cardiff University, School of Biosciences, Park Place, CF10 3TL, Cardiff, United Kingdom*

matt.berg@bris.ac.uk

Non-random mating is considered one way of promoting (or counteracting) polymorphism. For example, assortative mating is expected to reduce gene flow between morphs, leading to phenotypic divergence. Conversely, dissassortative mating may help to maintain rare or intermediate phenotypes. Ring species, where a chain of intermediate forms separates two relatively divergent forms, provide an excellent opportunity to study the processes leading to polymorphism and population divergence. We studied a parrot ring species, the crimson rosella (*Platycercus elegans*). Genetic analyses indicate a relatively close relationship between the members of this species complex, but this study is the most detailed so far of their phenotypic variation. We used spectrometry and visual observations to assess coloration in all of the main forms. In the area studied, the complex consisted of several forms defined primarily by their red-yellow coloration, including a chain of clinally varying intermediate populations. As expected, we found a high degree of overall colour differences between populations, and greater polymorphism in intermediate populations. To study the influence of sexual selection on this system, we report (1) the frequencies of colour morphs across populations, (2) sexual dimorphism and condition dependence of coloration, and (3) the occurrence of (non-)random mating with respect to coloration in intermediate populations, including a zone of presumed intergradation between the most divergent forms. We discuss whether sexual selection may contribute to colour polymorphism in this system, and whether colour polymorphism promotes reproductive isolation despite possibly considerable gene flow.

01-02 Poster

EVOLUTION ON THE DOT CHROMOSOME IN DROSOPHILA AMERICANA

Andrea J. Betancourt [1]

[1] *University of Edinburgh, Institute of Evolutionary Biology, King's Buildings, W. Mains Rd., EH93JT, Edinburgh, UK*

abetanco@staffmail.ed.ac.uk

Degenerate sex chromosomes are limited to a single sex and lack recombination, and each of these factors can independently have a profound effect on their evolution. The absence of recombination, for instance, may lead to slower rates of adaptation, reduced purifying selection, and depressed diversity, all factors that may contribute to the degenerative process. In the Drosophila genus, there is another chromosome with very little recombination, the dot chromosome, containing about 80 genes. Study of this autosomal chromosome offers an opportunity to examine the effect of the lack of recombination, independently of unisexual inheritance. To this end, I am examining evolution of genes on the dot chromsome of D. americana, and will present results showing how this chromosome suffers from evolutionary forces that may lead to degeneration.

01-03 Poster

EVOLUTION OF PIGMENTATION PATHWAYS BY GENE AND GENOME DUPLICATION IN FISH

Ingo Braasch [1], Jean-Nicolas Volff [2], Manfred Schartl [1]

[1] *University of Würzburg, Physiological Chemistry I, Biozentrum Am Hubland, D-97074, Würzburg, Germany*
[2] *Université de Lyon, Institut de Génomique Fonctionnelle, 46 allée d'Italie, F-69003, Lyon, France*

ingo.braasch@biozentrum.uni-wuerzburg.de

Teleost fishes are the most species-rich group of vertebrates. The unique diversity and complexity of pigmentation and color patterning observed in teleosts might play a major role in speciation since visual cues are very important for communication, species recognition and mating preference. Fishes underwent a whole genome duplication (fish-specific genome duplication; FSGD) early in their history so that two copies of many vertebrate genes are found within teleost genomes including genes known to be involved in pigment cell development such as *sox10*, *mitf*, *kit*, and *csf1r*. To gain more insights into the impact of the FSGD on evolution of pigmentation in teleosts, we have studied two major pigment synthesis pathways in fish, the melanin and the pteridine pathways, with respect to different types of gene duplication using a comparative genomic approach including phylogenetic and synteny analyses. Genes encoding three of the four enzymes involved in the synthesis of melanin from tyrosine have been retained as duplicates after the FSGD (*tyr, tyrp1, silv*). We have found evidence for divergent resolution of tyrosinase gene family members, *i.e.*, differential gene loss in divergent teleost lineages. In the pteridine pathway, two cases of duplicated genes originating from the FSGD as well as several lineage-specific gene duplications were observed. We have also found a previously unrecognized diversity of GTP-cyclohydrolase I genes in vertebrates that correlates with the presence and absence of xanthophores in different vertebrate groups. Our results support an important role of the FSGD and other types of duplication in the evolution of pigmentation in fish. Functional experiments on the differential evolution of pigmentation gene duplicates in divergent teleost lineages such as zebrafish, medaka, and poeciliids will complement these data with respect to the significance of gene and genome duplication for the evolution of teleost coloration and vertebrate phenotypes in general.

01-04 Poster

THE COLOUR OF MONKEYS: WHITE VS. PIGMENTED HAIR PATCHES IN PRIMATES ARE NOT ATTRIBUTABLE TO PATTERNS OF MELANOBLAST MIGRATION

Brenda J. Bradley [1], Jennifer Pastorini [2], Pierre Moisson [3], Mitchell Irwin [4], Toni Lyn Morelli [5], Nicholas I. Mundy [1]

[1] *University of Cambridge, Department of Zoology, Downing Street, CB2 3EJ, Cambridge, UK*
[2] *Centre for Conservation and Research, 35 Gunasekara Gardens, Rajagiriya, Sri Lanka*
[3] *Parc Zoologique et Botanique de la Ville de Mulhouse, 51 Rue du Jardin Zoologique, 68100, Mulhouse, France*
[4] *McGill University, Department of Biology, 1205 Docteur Penfield Avenue, H3A 1B1, Montreal, Canada*
[5] *Stony Brook University, Department of Ecology and Evolution, 11794, Stony Brook, NY, USA*

bjb37@cam.ac.uk

Primates are arguably the most colourful mammalian order, yet we know little about the genetic basis and evolution of primate pigmentation. The genetic basis of pigmentation in mice, however, is relatively well understood, and we generally assume that this ‘mouse model’ applies to pigmentation in most mammals, including primates. Primate species show many colour phenotypes similar to those seen in breeds of fancy mice, including distinctive white hair patches on the head or body (piebald, variegated). In mice, these white hairs usually lack melanocytes because the melanoblasts failed to migrate or survive in these regions during embryogenesis. Thus, in mice, the molecular basis of white hair patches is usually controlled by genes involved in melanocyte distribution. We examined gene expression patterns in follicles of white and pigmented hair tufts plucked from living monkeys and lemurs and checked for the presence of melanocytes via quantitative RT-PCR of a melanocyte marker gene (*MITF*). For all individuals, white hair follicles showed high *MITF* expression levels, similar to those of pigmented hair, indicating that white hair patches in these primates have functioning melanocytes. Several genes involved in pigment-synthesis (*MC1R, MGRN1, ATRN*) were also often expressed in white hairs of primates. This indicates that white hair patches in primates are likely due to genetic changes affecting the pigment-synthesis pathway, rather than the distribution of melanocytes.

01-05 Poster

EVOLUTION OF MELANIN WING PATTERNS DURING SPECIATION

Jonathan M. Brown [1]

[1] *Grinnell College, Biology, Noyce Science Center, 50112, Grinnell, IA, USA*

brownj@grinnell.edu

Patterns of melanin deposition on wings are commonly used for taxonomic identification in many groups of gallmaking flies in the family Tephritidae; however, neither the functional significance nor the mechanisms of evolutionary change in these characters have been well studied. Species vary in details of elaborate courtship behaviors, all of which include wing displays by males or both sexes; this suggests a potential role for wing pigmentation patterns in mate signaling. Since divergence in such patterns may be either a consequence or a mechanism of reproductive isolation, we have developed image analysis techniques to quantify within- and between species pattern variation in two tephritid study systems: (1) host races of the goldenrod ball gallmaker Eurosta solidaginis and (2) an endemic radiation of Trupanea species on the Hawaiian archipelago. Here I provide an overview of simultaneous studies of the wing divergence patterns and genetic differentiation of species and populations. I show that (a) host races of Eurosta solidaginis are significantly differentiated in wing patterns despite evidence for gene flow between them; (b) hybridization between non-host-differentiated geographical races of E. solidaginis suggests that relative large pattern differences evolved during geographic isolation do not act as absolute pre-mating barriers; (c) geographic isolation of Trupanea species on different Hawaiian islands results in divergence of wing patterns; (d) degree of sexual dimorphism in wing patterns varies significantly among Trupanea species, suggesting that evolution of mate signals is an important feature of some speciation events in this radiation; and (e) an increase in melanin desposition on wings in Hawaiian Trupanea is associated with shifts in larval feeding mode, from ancestral seed-feeding to the derived mode of feeding on plant vegetative tissues.

01-06 Poster

CANDIDATE GENES INVOLVED IN PLUMAGE COLOR VARIATION IN FICEDULA FLYCATCHERS.

Laura Buggiotti [1], Glenn-Peter Saetre [2], Craig R. Primmer [1]

[1] *University of Turku, Biology, Vesilinnantie, 5, 20014, Turku, Finland*
[2] *University of Oslo, Biology, 0371, Oslo, Norway*

laubug@utu.fi

Plumage color variation has recently received considerable research attention possibly due to the importance that melanin ornaments have in individual's mating success (sexual and social selection) and the evolutionary forces which had led to the variety of plumage coloration within species observed today. The bird species complex comprising the pied flycatcher *Ficedula hypoleuca* and the collared flycatcher *F. albicollis* were the focus of this study and they have a wide distribution range through Europe. The geographical distribution of *Ficedula* flycatcher forms suggest that a sympatric divergence in secondary sexual characters has occurred. Furthermore it has been suggested that in sympatry female choice selects for a character displacement of male plumage traits which helps species recognition and thus male plumage coloration is likely to contribute to pre-zygotic reproductive isolation. Consequently, pied and collared flycatcher have been used as model species to investigate whether three promising candidate genes for melanization, melanocortin-1 receptor (MC1R), agouti-related protein (AGRP), and tyrosinase-related protein-1 (TYRP1) could possibly be associated with the plumage color variation observed in sympatric and allopatric populations of *Ficedula* flycatchers. As these genes are mainly involved in the melanic plumage color pathway, an assessment of the amino acid sequence of these genes in relation to plumage color variation could potentially help in understanding the molecular bases for the different variety of plumage/pigmentation pattern.

01-08 Poster

PLASTICITY OF THE PHENOLOGY OF SPECIALIST AND GENERALIST BIRD SPECIES

Jean-Pierre Moussus [1], Joanne Clavel [2], Romain Julliard [1]

[1] *MNHN, Conservation Biology, 55 rue Buffon, 75005, Paris, France*
[2] *Paris 6/MNHN, Conservation biology, 55 rue Buffon, 75005, Paris, France*

jclavel@mnhn.fr

Specialized species of various groups have been found declining throughout the world. This poor success rate of specialists, with communities increasingly made of generalists, is part of the global process of biotic homogenization.

During the last decades, climate has noticeably changed and is forecasted to change even more in the current century. These profound climate modifications influence many organisms' life, particularly in seasonal environment: there, species have evolved in a predicable word so that their lifecycle matches those of their food. Today, climate change mismatches the synchronisation between trophic chains and could affected population viability. Some species are able to modify their phenology in response to climate variation while others are not.

The study of bird phenology is often labor-intensive (e.g., surveying laying date in hundreds of nest-boxes) or concerns a limited subset of species (e.g., migration date of species stopping over on a insular study site). We developed a method to estimate variation in the phenology using data from Breeding Bird Survey schemes (BBS) currently operating in many countries. We applied this method to the French BBS. We thus obtained for a wide range of species, comparable measure of the variability of the phenology of their lifecycle in spring (covering migration and start of the reproduction). We tested whether species with more or less limited ecological or climate niche have more or less plastic phenology. Taking account the phylogeny, we showed than generalist species were more variable than specialist species and thus more likely to cope with climate fluctuation.

Key-words: Climate change, specialist-generalist species, phenology, monitoring, Maximum likelihood.

01-09 Poster

WHY BE BLUE IN A SWAMP?

Becky Fuller [1]

[1] *University of Illinois, Department of Animal Biology, 104 Shelford Vivarium, 606 E. Healey St., IL 61820, Champaign, US*

fuller@life.uiuc.edu

A paradox exists in animal coloration: in some species, males exhibit color patterns that reflect in wavelengths that are poorly represented in the lighting environment. This is particularly so for male bluefin killifish, *Lucania goodei*. Males can have one of several color patterns on their anal fins, the most striking of which is blue, which occurs at high frequency in tea-stained swamps where ultraviolet and blue wavelengths (350-500 nm) do not transmit well. Not only is there less UV and blue light in swamps, but swamp animals are also less sensitive to UV and blue wavelengths and possess fewer UV and violet cone cells in their retinas in comparison to spring animals. All of these data raise the question as to why males should possess blue colors when viewed under swamp conditions. In this talk, I will present spectral data to distinguish between various hypotheses as to why males utilize blue anal fins in swamp conditions. The first hypothesis is that males trade-off brightness for increased contrast. Perceived brightness of blue anal fins can clearly not be greater in swamp populations. However, blue males may create high contrast with the water column or with other color elements on the body. Such contrast is detected most effectively by those photoreceptors whose sensitivity matches the background illumination. The second hypothesis is that blue fins represent a unique adaptation to the pressures of sexual and natural selection by serving as a private channel for communication. Blue signals may be effective over the short distances that males signal to conspecifics but may attenuate over longer distances such as those from which predators would view them. By combining estimates of genetic and environmental variability in both visual and reflectance properties, we can determine the manner in which the perception of male color patterns varies within and among populations.

01-10 Poster

PHENOTYPIC PLASTICITY IN INSECTS: THE EFFECTS OF SUBSTRATE COLOUR ON THE COLORATION OF TWO GROUND-HOPPER SPECIES

Jana Deppermann [1], Axel Hochkirch [1]

[1] *University of Osnabrück, Department of Biology/Chemistry, Barbarastr. 13, D-49076, Osnabrück, Germany*

hochkirch@biologie.uni-osnabrueck.de

The maintenance of variation is of crucial importance for the survival of populations and species. Colour polymorphism is a widespread phenomenon in animal taxa with strong consequences for microhabitat choice, predator avoidance, thermoregulation, life history strategies and mate choice. While studies on the ultimate causes for the evolution of colour polymorphism often assume a genetic determination of the colour morphs, environmental influences might also promote the maintenance of variation. Here we present data from a laboratory experiment to examine the influence of substrate colour on three aspects of the coloration of the two ground-hopper species *Tetrix subulata* and *Tetrix ceperoi*. We reared hatchlings either on dark or on light substrates, using a split-brood design. Our results show that colour morph frequencies differ between species, instars and substrates. In both species, black and dark olive colour morphs were found more frequently on the dark substrate, whereas the grey colour morph dominated on the light substrate. While the basic colour of the insects was strongly influenced by the background colour, the pattern of the pronotum changed mainly in response to the nymphal development. Our results falsify the hypothesis that discrete colour morphs co-evolve in concert with other life history traits. On the contrary, they suggest that the environmental conditions during the nymphal development influence the body coloration, which could affect the fitness of the adult insects substantially. Nevertheless, phenotypic plasticity is of high adaptive value as it enables the insects to adjust their coloration to the environmental conditions and increases their mimicry.

01-11 Poster

INVESTIGATING COLOUR POLYMORPHISM IN CORAL REEF FISH

Ben G. Holt [1], Isabelle M. Cote [2], Brent C. Emerson [1]

[1] *University of East Anglia, School of Biological Sciences, NR4 7TJ, Norwich, England*
[2] *Simon Fraser University, Department of Biological Sciences, 8888 University Drive, V5A 1S6, Burnaby, BC, Canada*

b.holt@uea.ac.uk

Marine radiations provide interesting systems to study species evolution as opportunities for allopatric speciation are limited by the lack of barriers to migration and by potential long distance larval dispersal. The teleost genus Hypoplectrus (Hamlets), distributed throughout the tropical western Atlantic, includes several distinct morphotypes, distinguished solely by their striking colouration. As yet, no other physical distinctions have been documented. Up to 8 colour forms can be found on a single reef, yet hamlets show strong assortative mating behaviour with respect to colour, and most morphs are currently classified as separate species. Despite these facts, independent molecular studies have consistently failed to clearly separate different hamlet species. We are investigating the evolution of Hypoplectrus morphotypes and have sampled throughout the distribution of these species. AFLP markers are being used to access the extent of gene flow between populations and search for loci which are potentially linked to colour type. We have also shown, using geometric morphometrics, that, whilst highly significant differences in body form are present between colour morphs, hamlet shape appears to be more closely associated with geographical regions. Stable isotope analysis of muscle tissue shows that different hamlet diets show large amounts of trophic overlap, with little evidence for distinct dietary niches between colour types. These results are inconsistent with proposed theories which suggest an ecological basis to the maintenance of these colour forms. These data compliment other ecological and behavioural data, produced by this project, and provide new insight regarding the existence of the Hypoplectrus polymorphism.

01-12 Poster

HUMANS MISINTERPRET COLOR CONTRASTS IN BIRDS

Olle Håstad [1], Anders Ödeen [2]

[1] *University of Bristol, School of Biological Sciences, Woodland Road, BS8 1UG, Bristol, UK*
[2] *Uppsala University, Department of Animal Ecology, Norbyvägen 18D, S-752 36, Uppsala, Sweden*

olle.hastad@bristol.ac.uk

Studies of animal color signals have traditionally relied on human color vision, potentially emphasizing spectral information differently from the intended receiver. We modeled retinal function to test whether human vision captures differences between color patches and individuals that are perceivable to a bird. Our results show that humans and birds disagree as to which pair of patches in the plumage of museum skins provides the strongest color contrast in 20% of 64 species, and which individual in a random pair is more colorful, defined as bearing the patch pair with stronger color contrast, in up to 19%. Models produced differences in perception between humans and both avian color vision systems (VS and UVS) and throughout the avian spectrum. Despite confirming a strong correlation between the human and avian color spaces, we conclude that a significant proportion of the information content in visual signals may be lost in translation.

01-13 Poster

EVOLUTION OF VENTRAL PLUMAGE MELANISM IN SKUAS (FAMILY STERCORARIIDAE): MC1R AND NEUTRAL MULTI-LOCUS PHYLOGENY

Kirstin Janssen [1], Nicholas I. Mundy [2]

[1] *Tromsø University Museum, Division for Natural History, 9037, Tromsø, Norway*
[2] *University of Cambridge, Department of Zoology, Downing Street, CB2 3EJ, Cambridge, United Kingdom*

Kirstin.Janssen@tmu.uit.no

The genetic basis of phenotypic change and adaptation is one of the major outstanding problems in evolutionary biology. Until recently it has been difficult to identify the genes involved, particularly in wild populations. However, the evolutionary conserved biochemical pathways of melanin-based fur and plumage pigmentation have become a promising model system with several candidate genes available to study the molecular basis of adaptation. One of these genes, the melanocortin-1-receptor gene (*MC1R*), has recently been shown to be associated with intraspecific melanism in several mammal and bird species. Our recent discovery that variation in the *MC1R*-gene is associated with melanism in arctic skuas (*Stercorarius parasiticus*) has generated an exceptional opportunity to resolve the evolutionary history of plumage variation to a degree not achieved before in any group of birds. Based on these findings, we are extending the study to investigate evolutionary genetics in the entire skua family (Stercorariidae), which comprises several species with conspicuous ventral plumage polymorphism and monomorphic congeners. Analyses of the *MC1R* gene in combination with a multi-locus phylogeny generated using neutral markers reveal that ventral plumage melanism has probably evolved independently at least twice within this family of seabirds, likely involving further pigmentation genes than the *MC1R*. Thus, our results illustrate that similar phenotypic changes may be generated by diverse genetic mechanisms even in closely related species.

01-14 Poster

EVOLUTION OF OPTICAL MICROSTRUCTURES ON THE WINGS OF BUTTERFLIES

Shelley Wickham [1, 2], Julia C. Jones [3], Tiziana Beninati [3], Maryanne C. J. Large [1, 2], Leon Poladian [2, 4, 5, 6],
Lars S. Jermiin [3, 5, 6]

[1] *School of Physics, University of Sydney, 2006, Sydney, Australia*
[2] *Optical Fibre Technology Centre, University of Sydney, 2006, Sydney, Australia*
[3] *School of Biological Sciences, University of Sydney, 2006, Sydney, Australia*
[4] *School of Mathematics & Statistics, University of Sydney, 2006, Sydney, Australia*
[5] *Sydney Bioinformatics, University of Sydney, 2006, Sydney, Australia*
[6] *Centre for Mathematical Biology, University of Sydney, 2006, Sydney, Australia*

lars.jermiin@usyd.edu.au

Many butterfly species possess ‘structural’ colour, where colour is due to optical microstructures found in the wing scales. A number of such structures have been identified on butterfly scales. In this study, we characterize the optical properties of different multi-layer structures found across a variety of species. The optical mechanism of suppression and exaggeration of angle-dependent optical properties (i.e., iridescence) of these structures is described. In addition, we consider the phylogeny of the butterflies, and are thus able to relate the optical properties of the structures to their evolutionary development. By applying different phylogenetic principles, we elucidate the evolutionary mechanisms of adaptation. For example, a simple parsimony analysis, in which all evolutionary changes are given equal weighting, implies convergent evolution of some structures; on the other hand, a Dollo parsimony analysis, in which the ‘cost’ of losing a structure is less than that of gaining it, implies that ‘latent’ structures can be reused.

01-15 Poster

THE EVOLUTION AND MAINTENANCE OF POLLEN COLOUR DIMORPHISMS IN NIGELLA DEGENII (RANUNCULACEAE)

Tove H. Jorgensen [1], Stefan Andersson [2]

[1] University of East Anglia, School of Biological Sciences, NR4 7TJ, Norwich, UK
[2] Lund University, Department of Ecology, Solvegatan 37, 22362, Lund, Sweden

t.jorgensen@uea.ac.uk

Flower colour can be a major determinant of plant fitness, not only because of preferential visitation by pollinators, but also because of pleiotropic relationships between the expression of floral pigments and biochemically related compounds that influence vegetative performance variables. As yet, few studies have examined the potential for selective forces, other than pollinators, to influence the relative fitness of different floral colour morphs. In a series of field, laboratory and greenhouse studies we determined the genetic and selective mechanisms underlying the origin and maintenance of variation in pollen colour in two subspecies of *Nigella degenii* (Ranunculaceae). The frequency of two colour morphs varies extensively in natural populations of the two subspecies. Furthermore, they have been genetically isolated for substantial periods of time and therefore provide a "replicated test" of the effect of natural selection.

Estimates of differentiation in pollen colour significantly exceeded the neutral expectations (estimated from AFLP data), suggesting that local adaptation has played a key role in the evolution of this monogenic character. We tested two sets of hypotheses to identify selective factors contributing to the maintenance of the colour variation. First, the role of selection on pollen colour during the pollination phase was investigated in natural and manipulated populations. Second, the role of genotype-by-environment interactions in the maintenance of colour variation was investigated in an extensive common-garden experiment involving both optimal and stressful conditions

01-16 Poster

EVOLUTIONARY DYNAMICS OF PHENOTYPIC AND GENETIC POLYMORPHISM

Sofia Caesar [1], Jonas Ahnesjö [1], Anders Forsman [1]

[1] Högskolan i Kalmar, Naturvetenskapliga institutionen, Barlastgatan 11, 39231, Kalmar, Sweden

Magnus.H.Karlsson@hik.se

Evolutionary theory postulates that natural selection will erode genetic variation. Fluctuations in population size, biased sex ratios and small population sizes may also result in loss of genetic variation. However, phenotypic polymorphisms (with a genetic underpinning) are common in nature. One general conclusion from theoretical investigations is that environmental variation could maintain genetic polymorphism.

pygmy grasshopper populations (*Orthoptera: Tetrigiade, Tetrix sp*) are usually polymorphic with regard to colour and pattern, despite the fact that they are subjected to many of the mechanisms believed to eliminate genetic variation. We use fire melanism as a model system to evaluate the role of environmental variation for the dynamics of polymorphism.

Pygmy grasshopper populations typically express fire melanism, meaning that after a fire event the frequency of black or dark coloured individuals is high. As succession proceeds the population becomes increasingly polymorphic.

There are three possible explanations for this: There is an initial advantage associated with dark coloured phenotypes, which disappears as spatial environmental complexity increases. There may be phenotypic plasticity for colour and pattern, or the colour morphs may express different migration patterns.

Here we present data for wild-caught and captive reared individuals collected to distinguish between these alternative hypotheses. We also discuss alternative directions for future research.

01-17 Poster

AVIAN CLOCK GENE POLYMORPHISM: EVIDENCE FOR A LATITUDINAL CLINE IN ALLELE FREQUENCIES

Arild Johnsen [1], Andrew Fidler [2], Bart Kempenaers [3]

[1] *University of Oslo, Norway*
[2] *Cawthron Institute, New Zealand*
[3] *Max Planck Institute for Ornithology, Seewiesen, Germany*

b.kempenaers@orn.mpg.de

In comparison with most animal behaviours, circadian rhythms have a well characterized molecular basis. Detailed studies of circadian clock genes in ‘model’ organisms provide a foundation for interpreting the functional and evolutionary significance of polymorphic circadian clock genes found within free-living animal populations. Here we describe allelic variation in a region of the avian *Clock* orthologue which encodes a functionally significant polyglutamine repeat (*Clk*polyQcds), within a free-living populations of two passerine birds, the migratory bluethroat (*Luscinia svecica*) and the predominantly non-migratory blue tit (*Cyanistes caeruleus*). Multiple *Clk*polyQcds alleles were found within populations of both species (bluethroat: 12 populations, 7 alleles; blue tit: 14 populations, 9 alleles). Some populations of both species were differentiated at the *Clk*polyQcds locus as measured by F_{ST} and R_{ST} values. Among the blue tit, but not bluethroat, populations we found evidence of latitudinal clines in (a) mean *Clk*polyQcds repeat length and (b) the proportions of three *Clk*polyQcds genotype groupings. Parallel analyses of microsatellite markers, considered selectively neutral, indicate that allelic variation at the *Clk*polyQcds locus is not simply a reflection of selectively neutral population processes. We suggest that the observed *Clk*polyQcds allelic variation is, at least in part, maintained by selection reflecting micro-evolutionary adaptation to photoperiodic parameters correlated with latitude.

01-18 Poster

MULTILOCUS PATTERNS OF NUCLEOTIDE DIVERSITY, LINKAGE DISEQUILIBRIUM AND DEMOGRAPHIC HISTORY OF NORWAY SPRUCE

Myriam Heuertz [1], Emanuele De Paoli [2], Thomas Källman [3], Hanna Larsson [3], Irena Jurman [2], Michele Morgante [2], Martin Lascoux [3], Niclas Gyllenstrand [3]

[1] *Université Libre de Bruxelles, Behavioural and Evolutionary Ecology, CP 160/12 50, Av. F.D. Roosevelt, B-1050, Bruxelles, BELGIUM*
[2] *Universita` di Udine, Agrarie ed Ambientali, 33100, UDINE, ITALY*
[3] *Uppsala University, Evolution, Genomics and Systematics, Norbyvägen 18D, 752 36, UPPSALA, SWEDEN*

thomas.kallman@ebc.uu.se

We have studied DNA polymorphism at 22 loci in 47 Norway spruce [Picea abies (L.) Karst.] haplotypes. The overall nucleotide variation was limited, being lower than that observed in most plant species so far studied. Mean observed Fst was 0.12, which is substantially higher compared to earlier studies using RAPD and isozyme markers. All populations, with the exception of the Romanian population, could be divided into two main domains, a Baltico-Nordic and an Alpine one. Multilocus neutrality tests based on Tajima´s D and Fay and Wu H led to the rejection of the standard neutral model and a model including exponential growth. On the other hand, the data are compatible with a severe bottleneck occurring some hundreds of thousands of years ago.

01-19 Poster

IS THERE SEXUAL SELECTION FOR PLUMAGE COLOURATION IN PIED FLYCATCHERS?

Paula K. Lehtonen [1], Toni Laaksonen [1], Craig R. Primmer [1]

[1] *University of Turku, Dept. of Biology, Vesilinnantie 5, 20014, Turku, Finland*

paula.lehtonen@utu.fi

The conspicuous colouration observed in many animals is thought to have evolved as a response to sexual selection. The pied flycatcher (Ficedula hypoleuca) is a small passerine bird in which males vary in their dorsal colouration along a continuum that ranges from brown to black. The frequency of darkly coloured males has been observed to increase with increasing distance from the nearest collared flycatcher (Ficedula albicollis) population. The observed pattern is hypothesised to have arisen as a consequence of fitness advantages that are gained from character displacement in areas of sympatry. In areas where the collared flycatcher does not occur, sexual selection is thought be the driving force that favours darkly coloured males, but little evidence supporting the sexual selection hypothesis has been found to date.

After successfully attracting a female to a territory, most pied flycatcher males will attempt to form a pair-bond with a second female to father two nests. Approximately 20% are successful. Additional paternities may be gained via extra-pair copulations that do not involve a social bond. If female pied flycatchers breeding in areas of allopatry prefer darkly coloured males over their lighter conspecifics, a darkly coloured male can be hypothesised to gain more matings and father more offspring than a light one.

The aim of this study is to examine the total reproductive output of each male within the study population in relation to colouration. Paternities have been determined using 5 polymorphic microsatellite markers that have been multiplexed in one PCR and provide a total exclusionary power of 99.4% when one parent is known. The results will be discussed.

01-20 Poster

MOLECULAR EVOLUTION OF THE DUPLICATED CAROTENOID BIOSYNTHETIC ENZYME LYCOPENE-BETA SYNTHASE IN FLOWERING PLANTS

Kevin Livingstone [1], Heather Highland [1], Hunter Bowen [1], Heather Franco [1]

[1] *Trinity University, Department of Biology, One Trinity Place, 78212, San Antonio, United States*

klivings@trinity.edu

Carotenoids are the plant pigments that play an essential role in photosynthesis and photoprotection and also confer red, orange, and yellow coloration to flowers and fruits. Experiments have shown that the developmental changes in flowers and fruits from green to red/orange/yellow coloration and between alternate colors affect their interactions with animals, therefore coloration is presumed to be under selection. Despite this prevailing belief, however, no experiments have shown that a specific change in fruit color was caused by selection, leaving open the question of whether selection on fruit color is the cause the observed diversity. Cultivated peppers (Capsicum annuum) and their close relatives accumulate the carotenoids capsanthin and capsorubin only in their fruits, and these compounds appear to cause a derived shift in mature fruit coloration. The gene responsible for the production of these compounds was cloned previously and shown to be a subfunctionalized duplicate of lycopene beta-cyclase, another carotenoid biosynthetic gene, The existence of this duplicate has been detected in multiple species within the Solanaceae; however, new database searches indicate this duplication may date closer to the root of eudicots. While both copies of this locus exist in many taxa, capsanthin-capsorubin synthase activity has not been seen in copies tested outside this lineage. Copies of both duplicates have been sequenced from a greater sample of Solanaceous species, and it appears that the duplicated locus is under purifying selection across ca. 80% of the coding region and neutral evolution across the rest. Tests are ongoing to determine which specific mutations are responsible for this novel biosynthetic capacity to answer the question of how much change at the molecular level is needed to generate a new biochemical phenotype and how this transition proceeded.

01-21 Poster

DO FEMALE STICKLEBACKS AND ARCTIC CHARR TRADE OFF VULNERABLE CAROTENOIDS BETWEEN ORNAMENTS AND EGGS?

Jarle Tryti Nordeide [1]

[1] *Bodø University College, Department of Fisheries and Natural Sciences, Mørkved, NO-8049, Bodø, Norway*

jarle.nordeide@hibo.no

The less extravagant carotenoids ornamentation of females compared to males, may be due to females', as opposed to males', investment of rare and vulnerable carotenoids in the gametes at the expense of ornaments. We tested this hypothesis in two different fishes, the three-spined sticklebacks (*Gasterosteus aculeatus*) and the Arctic charr (*Salvelinus alpinus*), where females of both species may have conspicuous carotenoids-based red coloration in their pelvic spines and belly, respectively. The results show a significant negative association between ornaments and eggs in sticklebacks, and a slightly non-significant negative association in charr. The red coloration seems not to be condition dependent in none of the species. Males choosing red coloured females will fertilise eggs with small amounts of carotenoids and appear not to gain any benefit from their mates' phenotypic quality that could result in offspring of improved quality. This may put a brake to further exaggeration of carotenoids-based ornamentation in females. These results do not support the "direct selection hypothesis" to explain the existence of the female ornaments.

01-22 Poster

THE POTENTIAL ADAPTIVE SIGNIFICANCE OF SHELL COLOR AND BODY PIGMENT POLYMORPHISMS IN THE INTERTIDAL SNAIL LITTORINA OBTUSATA

Megan Phifer-Rixey [1], Melanie Heckman [1], Geoffrey Trussell [2], Paul S. Schmidt [1]

[1] *University of Pennsylvania, Department of Biology, 415 S University Ave, 19104, Philadelphia, PA, USA*
[2] *Northeastern University, Marine Science Center, 430 Nahant Rd, 01908, Nahant, MA, USA*

mrixey@sas.upenn.edu

Patterns of color polymorphism can be striking signals of natural selection. The genus *Littorina* is noted for remarkable variation in shell color and patterning. Many hypotheses have been proposed to explain patterns of color polymorphism in *Littorina*, including visual predation, adaptation to physical stress, pleiotropy, and neutral processes. *Littorina obtusata* in the mid-intertidal region of the Gulf of Maine are highly polymorphic for shell color and experience substantial and predictable variation in temperature/desiccation stress. Shell color is expected to affect absorption of light and previous studies have linked patterns of shell color polymorphism to variation in thermal regimes in gastropods. We hypothesized that patterns of shell color morph frequencies in the Gulf of Maine are influenced by thermal regime.

In this study, we address the adaptive significance of shell color polymorphism in *L. obtusata* by evaluating patterns of color morph frequencies over thermal gradients at two spatial scales. We found that shell color frequencies vary clinally at both scales, patterns which contrast with variation in previously described reference loci. We also used an experimental, manipulative approach to test the functional relationship between shell color and fitness under ecologically relevant conditions. We found consistent differences in shell temperatures between color morph and that shell color predicts survival under hot, dry conditions. Our results suggest that clinal patterns of shell color morph frequencies in the Gulf of Maine are driven, at least in part, by thermally mediated selection. In addition, we describe clinal patterns in an additional morphological character, body pigmentation, and discuss the potential evolutionary significance of the trait.

01-23 Poster

PREENING-MEDIATED DEPOSITION OF UROPYGIAL GLAND WAX UNDERLIES THE IMMUNO-DEPENDENT RAPID CHANGE IN BILL COLORATION

Romain Piault [1]

[1] *University of Lausanne, Ecology and Evolution, Biophore Building, 1015, Lausanne, Switzerland*

romain.piault@unil.ch

Variation in body condition can cause rapid change in coloration in traits used in sexual selection and parent-offspring communication. The underlying mechanisms usually involve pigments, biological nanostructures, and blood flux. Behaviourally-mediated deposition of substances on the external body surface has been proposed as an alternative mechanism that can generate covariation between condition and coloration. It has been proposed that in birds preen wax spread on feathers using the bill might affect bill and plumage coloration. We therefore evaluated the hypothesis that variation in condition due to diseases results in preening-mediated changes in bill coloration. Using tawny owls (*Strix aluco*) whose bill is free of carotenoids, pigments known to mediate infection-induced changes in bill coloration, we induced immune challenges of different intensities to determine whether they differentially cause a change in bill coloration. We injected nestlings with lipopolysaccharides (LPS) or phytohaemagglutinin (PHA); LPS is known to reduce individual condition to a larger extent than PHA by inducing a more intense and thus costly immune response. Individuals immunized with LPS showed higher bill brightness than nestlings injected with PHA. Since we found that preen wax causally reduces bill brightness, this difference in coloration between treatments is probably due to a lower quantity of preen wax deposited on the bill of LPS-injected nestlings. This may result from a decreased investment in preening activities and/or decreased wax production, since LPS impaired the development of the uropygial gland. Our findings provide a behavioural mechanism to explain short-term variation in the intensity of colourful condition-dependent signals.

01-24 Poster

EVOLUTION OF THE MELANOCORTIN-1 RECEPTOR AND PLUMAGE COLOUR IN SWANS

Marie A. Pointer [1], Nick I. Mundy [1]

[1] *University of Cambridge, Dept. of Zoology, Downing Street, CB2 3EJ, Cambridge, United Kingdom*

map50@cam.ac.uk

Recently, substantial progress has been made in defining the genetic basis of variation in melanin-based coloration in wild birds. Non-synonymous changes within the Melanocortin 1 receptor (MC1R) gene have been linked to intraspecific melanic variation in bananaquit, lesser snow goose and arctic skua. In this study, we address whether MC1R also underlies interspecific variation in melanin coloration, using true swans (Cygnus) as a model system. Within the genus Cygnus, there is substantial variation in the distribution of black eumelanin among different species. C. columbianus, C. cygnus and C. olor, all have completely white adult plumage, whereas C. atratus has completely black plumage. Another species, C. melancoryphus has an intermediate phenotype-mostly white but with black feathers covering the neck and head. The entire coding sequence of MC1R and 300 bp of 5' UTR were sequenced from swans and a number of goose species serving as outgroups. Independent molecular phylogenies were generated from cytochrome B and lactate dehydrogenase gene sequences. Interestingly, key amino acid sites in MC1R that are important for a melanic phenotype are substituted in C. atratus and C. melancoryphus but are absent from the white species of Cygnus. In C. melancoryphus, a Glu94Lys substitution is found at the same position where a mutation is known to cause a dark phenotype in mouse, bananquit, chicken and quail. The completely black C. atratus has a Arg233His substitution shared with melanic rock pocket mouse and arctic skua, consistent with the melanic phenotype of this species. However, the substitution is also found in a distantly related outgroup species, the Coscoroba goose (Coscoroba coscoroba), which displays completely white plumage, which is most simply explained by mutation(s) at other loci. Overall, the results strongly suggest that MC1R variation is involved in plumage colour evolution among swan species, but further results will be necessary to confirm this.

01-25 Poster

THE GENETIC BASIS OF ADAPTIVE PIGMENTATION VARIATION IN DROSOPHILA MELANOGASTER

John E. Pool [1], Charles F. Aquadro [2]

[1] *University of Copenhagen, Centre for Comparative Genomics, Universitetsparken 15, bygn. 10, 2100, Copenhagen, Denmark*
[2] *Cornell University, Molecular Biology and Genetics, 233 Biotechnology Building, 14853, Ithaca, New York, United States*

jpool@bi.ku.dk

In a broad survey of Drosophila melanogaster population samples, levels of abdominal pigmentation were found to be highly variable and geographically differentiated. A strong positive correlation was found between dark pigmentation and high altitude, suggesting adaptation to specific environments. DNA sequence polymorphism at the candidate gene ebony revealed a clear association with the pigmentation of homozygous third chromosome lines. The darkest lines sequenced had nearly identical haplotypes spanning 14.5 kilobases upstream of the protein-coding exons of ebony. Thus, natural selection may have elevated the frequency of an allele that confers dark abdominal pigmentation by influencing the regulation of ebony.

01-26 Poster

WHAT A MULTIVARIATE QUANTITATIVE GENETIC APPROACH CAN TELL US ABOUT THE EVOLUTION OF SEXUAL COLOURATION

Erik Postma [1]

[1] *University of New South Wales, School of Biological, Earth and Environmental Sciences, NSW 2052, Sydney, Australia*

e.postma@unsw.edu.au

Despite a growing awareness that organisms are not one-dimensional, the great majority of studies on the evolution of colour traits continues to reduce an animal’s phenotype to a single measurement of one single trait. Evidence is however rapidly accumulating that this univariate approach provides us with an overly simplistic description of an individual’s phenotype, which is unable to advance our understanding of the evolution of coloration and of complex phenotypes in general. For example, different traits, but also different aspects of the same trait, may provide different types of information, and correlations among them may severely limit there evolutionary trajectory. A number of recent developments in multivariate quantitative genetics has now provided us with a powerful set of tools to analyse the genetics underlying colour signals, and to describe the correlations among them. This can provide us with the relative roles of genes and environment in shaping variation in coloration, and it allows for the identification of the major axes along which selection can operate. Finally, it allows us to directly test for associations between the major axes of both genetic and environmental variation on the one hand, and independent measures of quality and attractiveness on the other. In this talk I will outline how a multivariate quantitative genetic analysis can help us understand the evolution of coloration, and I illustrate this with data from two large-scale breeding experiments with guppies and zebra finches.

01-27 Poster

SPAWNING COLOR DIVERGENCE REFLECTS LOCAL ADAPTATION AMONG SOCKEYE SALMON

Kristina M. Ramstad [1], Carol A. Woody [2], Fred W. Allendorf [3]

[1] *Victoria University of Wellington, School of Biological Sciences, P.O. Box 600, 6140, Wellington, New Zealand*
[2] *U.S. Geological Survey, Alaska Science Center, 4230 University Drive, Suite 201, 99508, Anchorage, Alaska, USA*
[3] *Division of Biological Sciences, University of Montana, 32 Campus Drive, 59812, Missoula, Montana, USA*

kristina.ramstad@vuw.ac.nz

Sockeye salmon (*Oncorhynchus nerka*) display dramatic secondary sexual traits during spawning, including red body color that is carotenoid-based and highly heritable. We examined variation in body and egg color among thirteen sockeye salmon populations in Lake Clark, Alaska and found evidence for adaptive color differences between fish spawning in glacial and non-glacial habitats. Lake Clark sockeye salmon populations arose from a single founding event between 100 and 400 hundred generations ago and exhibit low genetic divergence at 11 microsatellite loci ($F_{ST} < 0.024$) that is uncorrelated with spawning habitat type. We found a higher frequency of pink females spawning in glacial habitats with high turbidity. The lighter pink rather than red body color is possibly due to reduced sexual selection for red spawning color in highly turbid water with low visibility. Females with lighter pink body color tended to have darker eggs, apparently due to a trade-off in carotenoid allocation between body and egg color in females. In contrast to females, nearly all males exhibited bright red body color in all habitat types. Mean P_{ST} (phenotypic divergence among populations) exceeded neutral F_{ST} for female body color, but was less than neutral F_{ST} for male body color. This suggests (1) that body color differences between fish spawning in glacial and non-glacial habitats could not be explained by genetic drift alone and (2) that selection favors different body colors in glacial (pink) and non-glacial (red) spawning females and red body color among males spawning in both habitat types. Our data provide the first evidence of adaptive color polymorphism among sockeye salmon.

01-28 Poster

USING MUTANTS TO UNDERSTAND THE PRINCIPLES OF WING PATTERN FORMATION IN BUTTERFLIES

Suzanne Saenko [1], Paul Brakefield [1], Patricia Beldade [1]

[1] *Institute of Biology / Leiden University, Evolutionary Biology, Leiden, The Netherlands*

s.v.saenko@biology.leidenuniv.nl

Butterfly wing patterns are ideally suited for studying interactions between the evolutionary and developmental processes that generate morphological variation in natural populations. The African butterfly *Bicyclus anynana* (Nymphalidae: Satyrinae) with its conspicuous eyespots has been established as an “evo-devo” laboratory model and successfully used to study the genetic mechanisms underlying variation in eyespot patterns. Identification of the genes involved in colour pattern formation, however, remains a challenge because genomic resources for this species are only starting to be developed. Moreover, none of the well-studied insect model species has eyespot patterns which appear to be a Lepidoptera-specific trait.

Mutants have been successfully used to study developmental mechanisms of various morphological traits in different species. In our laboratory we maintain a large stock of *Bicyclus anynana* butterflies where mutants that affect different aspects of wing pattern appear spontaneously from time to time. Here we present the results of our research on the *Comet* mutant that has a pleiotropic effect on eyespot shape, parafocal elements and male androconial structures.

01-29 Poster

CAROTENOID COLORATION IN GREENFINCHES IS INDIVIDUALLY CONSISTENT IRRESPECTIVE OF FORAGING ABILITY

Lauri Saks [1], Ulvi Karu [1], Peeter Hõrak [1]

[1] *Tartu University, Institute of Zoology and Hydrobiology, Vanemuise 46, 51014, Tartu, Estonia*

slauris@ut.ee

Carotenoid-based plumage coloration of birds has been hypothesised to honestly reflect individual quality either because carotenoids are difficult to acquire via food or due to trade-off between allocation of carotenoids between maintenance and signalling functions. We tested whether differential foraging ability is a necessary precondition for maintaining individual differences in carotenoid-based plumage coloration in male greenfinches (*Carduelis chloris*). Wild-caught birds were brought into captivity where half of them were supplemented with carotenoids while the other half was maintained on a carotenoid-poor diet. Colour of the yellow parts of tail feathers, grown under natural conditions was compared with that of the replacement feathers, grown in captivity. Carotenoid-supplementation increased feather chroma (saturation). Colour of wild-grown feathers significantly correlated with the colour of lab-grown feathers. This result demonstrates the existence of a significant component of variation in carotenoid coloration which reflects differences in genetic and/or physiological qualities among individuals independently of foraging ability. Among both experimental groups, plasma carotenoid concentration during feather growth strongly correlated with chroma of the feathers grown in captivity. This indicates that carotenoid-based plumage coloration can reveal circulating carotenoid levels over a very wide range of concentrations, suggesting the ample signalling potential of such a mechanism.

01-30 Poster

A QTL ANALYSIS OF MALE SONG AND FEMALE ACOUSTIC PREFERENCE SUPPORTS THE PLEIOTROPIC MODEL OF MATE RECOGNITION EVOLUTION IN HAWAIIAN CRICKETS

Kerry L. Shaw [1]

[1] *University of Maryland, Biology, Biology/Psychology Building, 20742, College Park, Maryland, USA*

kerryshaw@umd.edu

The pleiotropic model of mate recognition evolution predicts that male and female phenotypes share a common genetic control, wherein selective pressure to keep the communication system functional is aided by the co-inheritance of genetic factor(s) underlying the communication phenotypes. In contrast, the coevolutionary model predicts a genetic correlation caused by assortative mating or selection on the efficacy of the communication process. In the Hawaiian cricket genus Laupala, both male calling song and female acoustic preference have diverged rapidly. We conducted a QTL mapping study of variation in male calling song and female acoustic preference between two close relatives, L. paranigra and L. kohalensis, to test the pleiotropic model of acoustic communication. The eight small to moderately sized QTL for song showed evidence of directional selection. A QTL for female acoustic preference co-localized to a region for song, supporting the pleiotropic model of mate recognition evolution.

01-31 Poster

RECURRENT MUTATION IN A SPATIAL SINGLE-LOCUS SELECTION MODEL

Bastiaan Star [1], Hamish Spencer [1]

[1] *University of Otago, Zoology, 340 Great King Street, Dunedin, New Zealand*

bastiaanstar@hotmail.com

Models that ‘construct’ genetic polymorphism by introducing mutations to a population of alleles show that this iterative process can easily lead to the stable maintenance of moderate levels of polymorphism, regardless of the fact that the corresponding proportion of fitness space that leads to a stable polymorphism is vanishingly small. These constructionist models have never been studied in a spatial context before and it is not known wether different levels of gene flow affect the construction of selectively maintained genetic polymorphism in a heterogeneous habitat. The present study investigates the effect of a heterogeneous habitat by simulating recurrent mutation in a spatial viability-selection model with different levels of gene flow. Low levels of gene flow result in higher levels of polymorphism whereas high levels of gene flow result in lower levels of polymorphism when compared to a single-deme model. Low levels of gene flow facilitate alleles with more locally adapted fitness sets whereas high levels of gene flow facilitate alleles that have more co-adapted fitnesses in both demes. Moreover, gene flow has a large influence on the ease with which the system can be invaded by new alleles, with an intermediate level of gene flow being most conducive to invasion. Multi-deme viability systems can have polymorphic equilibria that are locally stable rather than globally, and the constructionist approach results in more stable equilibria than is expected from a fitness-space or equilibrium based approach.

01-32 Poster

THE ECOLOGY AND EVOLUTION OF ASSOCIATED MICRO-ORGANISMS IN THE TERMITE-TERMITOMYCES MUTUALISM

Anna A. Visser [1], Duur K. Aanen [1], Alfons J. M. Debets [1], Thomas W. Kuyper [2], Rolf F. Hoekstra [1]

[1] *Wageningen University, Laboratory of Genetics, Arboretumlaan 4, 6703 BD, Wageningen, The Netherlands*
[2] *Wageningen University, Department of Soil Quality, Droevendaalsesteeg 4, 6708 PB, Wageningen, The Netherlands*

Anna.Visser@WUR.nl

Fungus-growing termites (subfamily Macrotermitinae) cultivate Basidiomycete fungi (of the genus *Termitomyces*) for food. They are mutually dependent. The cultivar is grown in single-strain monocultures that are clonally propagated within the termite nest. What mechanisms operate in termite nests that sustain a stable monoculture, suppressing everything except *Termitomyces*?

Species of the Ascosmycete genus *Xylaria*, for instance, are associated with the mutualism. They are unnoticed in living termite nests. However, they occur in dead termite nests and on fresh nest material that is incubated in the absence of termites very frequently. In addition various other fungi have been isolated from termite nest material. What role do they play? Are they opportunists, or have certain species specialised in inhabiting termite nests?

To address these questions, termite mounds of three species of *Macrotermes* in different locations in South-Africa were investigated. *Xylaria* species, other fungi and bacteria were isolated. Their distribution on different spatial scales was examined. A phylogenetic tree of all *Xylaria* species that were found was made based on ITS sequences. This tree was compared with phylogenetic trees of the termites and *Termitomyces*. Complementary trees would prove *Xylaria* species to be specialised inhabitants of termite nests. Moreover, they may have coevolved with the termite-*Termitomyces* mutualism. Thus far, specialisation of *Xylaria* appears ambiguous.

Additional fieldwork has been performed to define the role of *Xylaria*. Ultimately this research seeks to explain the evolution and evolutionary stability of the ecology in the termite nest.

01-33 Poster

INVESTIGATING ECOLOGY OF COLORATION USING THE GENETICS OF COLOUR VISION

Anders Ödeen [1], Olle Håstad [2]

[1] *Uppsala University, Department of Animal Ecology, Norbyvägen 18D, S-752 36, Uppsala, Sweden*
[2] *University of Bristol, School of Biological Sciences, Woodland Road, BS8 1UG, Bristol, United Kingdom*

anders.odeen@ebc.uu.se

Colour vision in diurnal birds may be categorized into two classes: VS with a short-wavelength sensitivity biased toward violet and UVS biased toward ultraviolet. We have pioneered an expeditious molecular method to estimate the colour sensitivities of a bird by sequencing a part of the gene coding for the ultraviolet absorbing SWS1 retinal opsin. With this method, we demonstrate that the distribution of colour vision among diurnal birds is quite complex. For example, the spectral sensitivities of raptors and corvids (VS), which are important predators of Passerida songbirds, are significantly different from that of their prey (UVS). While sexual selection favours brighter coloration in the signalling sex, increased exposure to predators will select against conspicuous coloration. But given the retinal differences, Passerida males should be selected to reduce their conspicuousness to their predators without lowering the attractiveness of the plumage coloration to conspecifics. Using a model of retinal physiology, we have tested whether plumage colours of Passerida males will be perceived as more different from the natural background of their breeding habitat when viewed by conspecifics than when viewed by a raptor or corvid predator. We also test whether sexual dichromatism in Passerida species becomes more pronounced when males and females are observed through their own vision system than that of raptors and corvids.

01-34 Poster

COLONIZING A DESERT WETLAND: POPULATION HISTORY OF THE NILE CROCODILE IN SOUTH-CENTRAL AFRICA REPRESENTS A BIOTIC SIGNATURE FROM AN ANCIENT PALAEO-LAKE

Jacqueline M. Bishop [1, 2], Patrick Aust [3], Fenton P. D. Cotterill [4], Alison J. Leslie [2], Colleen O'Ryan [1]

[1] *University of Cape Town, Molecular & Cell Biology, Private Bag, 7700, Cape Town, South Africa*
[2] *University of Stellenbosch, Conservation Ecology & Entomology, Private Bag, 7602, Stellenbosch, South Africa*
[3] *Imperial College, Division of Biology, Silwood Park, Ascot, SL5 7PY, Berkshire, England*
[4] *University of Cape Town, Africa Earth Observatory Network (AEON), Private Bag, 7700, Cape Town, South Africa*

bishop@sun.ac.za

Persistent uplift of Africa since the Cretaceous has disrupted drainage networks and maintained inland lakes within the Kalahari basin. Today, the Okavango Delta occupies a fault-controlled depression in south-central Africa that is maintained primarily by seasonal inflow but still retains ephemeral links with neighbouring drainage systems originally shared during the Plio-Pleistocene. In this study, we integrate analyses of nuclear and mitochondrial data to investigate whether populations of the Nile crocodile, *Crocodylus niloticus*, within the Okavango Delta and the neighbouring Upper Zambezi and Chobe Rivers reflect influences of landscape evolution across this dynamic drainage basin. Microsatellite data indicates the presence of shared lineages while sequence data suggests a sustained period of population growth across the region that peaked approximately one million years ago (95% C.I. 460 to 1600 Kya). This discovery suggests that extant populations of Nile crocodiles in the Delta and neighbouring rivers may represent the vestiges of a much larger population, which originally exploited the ancient Palaeo-Lake Makgadikgadi (PLM). Evidence constrains the tenure of PLM to the late Pliocene and early Pleistocene, and reveals its desiccation initiated at least 500 Kya. We propose a model where extant lineages are remnants of dispersal events that occurred over hundreds of thousands of years as wetlands became intermittently linked during periods of increased flooding, allowing crocodiles to move between what are today isolated systems.

01-35 Poster

ABSENCE OF INBREEDING DEPRESSION DESPITE UNPRECEDENTED SCALE OF DEMOGRAPHIC BOTTLENECK IN WHITE RHINOCEROS (CERATOTHERIUM SIMUM SIMUM)

Natalie J. Coutts [1], Jacqueline M. Bishop [2], Colleen O'Ryan [1], Janet L. Rachlow [3]

[1] *University of Cape Town, Molecular and cell biology, Private bag, Rondebosch, 7700 Cape Town, South Africa*
[2] *University of Stellenbosch, Conservation Ecology & Entomology, 7603 Cape Town, South Africa*
[3] *University of Idaho, Fish and Wildlife Resources, Moscow, ID 83844-1136, Idaho, USA*

colleen.oryan@uct.ac.za

The southern white rhinoceros (*Ceratotherium simum simum*) was at the brink of extinction as a result of uncontrolled hunting and habitat destruction throughout its historical range with ~100 animals surviving in South Africa. Here conservation efforts resulted in the species' protection and recovery with 90% of the remaining ~11000 rhinos resident in South Africa. New populations have been established in reserves across southern Africa, all sourced from the original surviving population. In this study we test the hypotheses that (i) extant populations of white rhinoceros will exhibit genetic evidence of their demographic bottleneck, and (ii) founder events will result in reduced genetic diversity and levels of differentiation among seeded. We analysed data from ten microsatellite loci for 176 animals that represent both the South African population (Umfolozi-Hluhluwe Complex) and three seeded populations in southern Africa (Waterberg Reserve in Namibia, Welgevonden Reserve in South Africa and Matobo National Park in Zimbabwe). Despite the extraordinary decline of the species no evidence of a genetic bottleneck was detected. It is noteworthy that the diversity in the white rhinoceros is lower than that seen in any other rhinoceros species. All seeded populations had reduced levels of heterozygosity relative to the source population. With the exception of Waterberg, all populations showed a positive F_{IS} suggestive of inbreeding within populations but this has not lead to decreased fecundity. Both pairwise F_{ST} and R_{ST} were similar were found to be highest among the seeded populations. This study provides baseline genetic information about this important species as well as insight into the genetic outcomes associated with demographic recovery after a bottleneck.

01-36 Poster

LONG-TERM PERSISTENCE OF ORIBATID MITES IN HETEROGENEOUS SOIL ENVIRONMENTS

Ina Schaefer [1], Katja Domes [1], Roy A. Norton [2], Stefan Scheu [1], Mark Maraun [1]

[1] *TU-Darmstadt/Biology, Zoology, Schnittspahnstr. 3, 64287, Darmstadt, Germany*
[2] *State University of New York, College of Environmental Science and Forestry, 1 Forestry Drive, NY 13210, Syracuse, USA*

schaefer@bio.tu-darmstadt.de

The fossil record reflects the origin, diversification and extinction of major groups of organisms. Oribatid mites, a diverse group of soil-living arthropods, have persisted throughout geological and paleontological changes. We applied a molecular clock approach to estimate the origin of oribatid mites and the age of large parthenogenetic clusters, which probably radiated while being parthenogenetic. Using fossil dates and 18S rDNA sequences, our study revealed that oribatid mites originated in the late Precambrian and that the major splits in this group are several hundred million years old, and therefore evolved and diversified over a very long period. Our molecular data confirm the fossil-based opinion that all major lineages of oribatid mites were established before the Jurassic. Survival and radiation combined with only moderate morphological changes of these lineages suggests that the basic structure of their niches remained constant throughout their evolutionary history. Presumably, niches in decomposing plant material changed little despite major turnover of the types of vegetation covering the earth's surface. The consistency of niches of oribatid mites likely also explains why they consist of a number of parthenogenetic lineages which radiated and formed several clades of "ancient asexual scandals".

01-37 Poster

POPULATION STRUCTURE AND COMPATIBILITY BETWEEN SUSCEPTIBLE AND INSECT RESISTANT BARBAREA VULGARIS

Fiorello Toneatto [1], Jens K. Nielsen [2], Sven B. Andersen [3], Thure P. Hauser [1]

[1] *University of Copenhagen, Faculty of Life Sciences, Department of Ecology, Rolighedsvej 21, 1958, Copenhagen, Denmark*
[2] *University of Copenhagen, Faculty of Life Sciences, Department of Natural Sciences, Thorvaldsensvej 40, 1871, Copenhagen, Denmark*
[3] *University of Copenhagen, Faculty of Life Sciences, Department of Agricultural Sciences, Thorvaldsensvej 40, 1871, Copenhagen, Denmark*

fit@life.ku.dk

The crucifer *Barbarea vulgaris* occurs in Denmark in two morphological types. One, the G-type (glabrous), is resistant to most populations of a specialist flea beetle *Phyllotreta nemorum*, the other, the P-type (pubescent), is susceptible. Resistant and susceptible types grow in separate and stable populations, where hybrids are rarely found. As part of an ongoing effort, we study the origin and evolution of the interaction between plant types and insects, by asking whether the G and P types originated in Denmark or elsewhere, and whether the two types are sexually compatible. To solve these questions, we analyze genetic and morphological population structure and insect resistance in twenty European populations, and paternity of offspring from an experimental mixed population of P and G-type plants. Preliminary results show that most of the European populations are glabrous, suggesting that the P-type is common only in Denmark. Further tests will show if the absence of hairs in the G-type is associated with insect resistance also outside Denmark. Paternity results show that there is low compatibility between P and G-type. Mother plants of the G-type produce 91% G-type offspring, and P-type mothers 87% P-type offspring.

2

Conservation genetics: genetic deterioration and adaptation to changing environments

Wednesday August 22 *Location*: Ekonomikum 4

Symposium 2: Conservation genetics: genetic deterioration and adaptation to changing environments

ORGANIZERS: Kuke Bijlsma, University of Groningen, The Netherlands
Volker Loesckcke, Aarhus University, Denmark
(sponsored by ESF progamme ConGen)

09.45-10.15	**Juan Bouzat** (invited) Natural selection and the purging of deleterious recessive alleles: effects of inbreeding history, inbreeding rate and inbreeding environment
10.15-10.45	**Markus Fischer** (invited) The role of neutral and adaptive evolution for plant conservation genetics in the heterogeneous cultural landscape
10.45-11.05	**Kuke Bijlsma** The interplay between genetic and environmental stress
11.05-11.35	*Coffee*
11.35-11.55	**Leonard Nunney** Survival or extinction: how fast can the red queen run?
11.55-12.15	**Audrey Zannese** Population responses to inbreeding and environmental perturbations: an experimental study
12.15-12.35	**Shu-Rong Zhou** The evolution of inbreeding depression in a metapopulation
12.35-14.00	*Lunch, council*
14.00-14.30	**Torsten N. Kristensen** (invited) Inbreeding and environmental stress – investigated on different levels of biological organization using Drosophila as a model organism
14.30-14.50	**Kamilla S. Pedersen** Proteome signatures of inbreeding and heat stress in Drosophila melanogaster
14.50-15.10	**Tarmo Ketola** Inbreeding increases resting metabolic rate and reduces energy available for allocation
15.10-15.30	**Marta Szulkin** Inbreeding-by-environment interactions in a wild bird population
15.30-16.00	*Coffee*
16.00-16.20	**Mårten B. Hjernquist** The magnitude of inbreeding depression decreases with environmental stress as female collared flycatchers change their reproductive strategy
16.20-16.40	**Lyanne Brouwer** Heterozygosity-fitness correlations in a bottlenecked island species; a case study on the Seychelles warbler
16.40-17.00	**Roosa Leimu** Genetic history, habitat quality and past selection as determinants of inbreeding and outbreeding depression in herbivore resistance and fitness of fragmented plant populations
17.00-17.20	**Andrea R. Pluess** Decreased plant viability due to genetic erosion in a fragmented landscape

02-01 Talk

NATURAL SELECTION AND THE PURGING OF DELETERIOUS RECESSIVE ALLELES: EFFECTS OF INBREEDING HISTORY, INBREEDING RATE AND INBREEDING ENVIRONMENT.

Juan L. Bouzat [1]

[1] *Bowling Green State University, Biological Sciences, Life Sciences Building, 43403, Bowling Green, Ohio, USA*

jbouzat@bgnet.bgsu.edu

An important issue in conservation biology is the extent to which natural selection can "purge" deleterious recessive alleles causing inbreeding depression. Although considerable experimental evidence exists regarding the role of inbreeding in decreasing fitness, there has been limited empirical data to suggest that purging plays any important role in small populations. Recent experiments in our lab evaluated the role of inbreeding history, inbreeding rate, and inbreeding environment on the effectiveness of selection in decreasing levels of inbreeding depression. These studies provide empirical evidence that indicate selective purging is more likely to occur in populations that had a prior history of inbreeding (e.g., through recurrent demographic bottlenecks). In addition, they show that purging is more effective in larger populations, which experience inbreeding at slower rates, and in populations exposed to stressful environments. These results suggest that selective purging may be more common than previously believed; limiting the threat that inbreeding depression may pose to population viability and persistence.

02-02 Talk

THE ROLE OF NEUTRAL AND ADAPTIVE EVOLUTION FOR PLANT CONSERVATION GENETICS IN THE HETEROGENEOUS CULTURAL LANDSCAPE

Markus Fischer [1, 2]

[1] *University of Bern, Institute of Plant Sciences, Altenbergrain 21, 3013 Bern, Switzerland*
[2] *University of Potsdam, Institute of Biochemistry and Biology, Maulbeerallee 1, 14469, Potsdam, Germany*

markus.fischer@ips.unibe.ch

In the cultural landscape environmental variation is characterised by natural and anthropogenic heterogeneity, which includes natural and land-use mediated environmental gradients, and fragmentation. It is often stated that plants may respond to environmental heterogeneity plastically and/or by adaptation. However, this dichotomy is not really useful, because plasticity may be adaptive itself, and because adaptation is of course not the only evolutionary pathway which affects plant fitness in the heterogeneous landscape. The latter is especially important because habitat fragmentation divides many plant species into small and isolated populations. There, genetic variation generally is reduced because of more pronounced genetic drift. This brings about a number of negative consequences for plant fitness. With few exceptions, the issues of adaptation and of selectively neutral forces such as inbreeding and genetic drift have been studied separately in conservation genetics. Ultimately, however, we need to understand their interaction. This is especially apparent in the question whether small and isolated populations are less well adapted than large ones. Moreover, it matters for the consequences of gene flow between populations, which promises a remedy for problems caused by reduced genetic variation but may compromise adaptation. I use case studies from my group to illustrate these issues and to put them in the wider context of the research agenda of conservation genetics.

02-03 Talk

THE INTERPLAY BETWEEN GENETIC AND ENVIRONMENTAL STRESS

Kuke (R.) Bijlsma [1]

[1] *University of Groningen, Population & Conservation Genetics, Evolutionary Genetics, P.O. Box 14, 9750 AA, Haren, Netherlands*

r.bijlsma@rug.nl

From an evolutionary perspective, stress is generally defined as an environmental factor that impairs Darwinian fitness. This at first sight simple definition, however, conceals a complex matter as stress is not only an attribute if the external and internal environment, but also an attribute of the organism experiencing that environment. Consequently, an environment, and changes therein, can be perceived differently by different genotypes, while, on the other hand, changes in the genetic architecture of organisms can alter the perception of a constant environment. This results in a complex interaction between genotype and environment, often causing synergistic effects, and both should, therefore, be studied integrative. In a man-dominated world, many species have to cope with stressful deteriorating environmental conditions, e.g. thermal stress for ectotherms. At the same time species are subject to genetic stress due to fragmentation, isolation and small population sizes, resulting in fitness depression and changes in the genetic architecture.

By using *Drosophila* as a model organism, we are studying the complex interactions between genotype and stress environments. On the on hand, we investigate changes in stress tolerance brought about by changes the genetic architecture of *Drosophila* by inbreeding. On the other hand, we investigate the fitness response of certain inbred lines in different stress environments. By integrating the results of the different experiments we hope to get better insights into the genes involved in stress tolerance, into how organisms cope with environmental stress, and how genetic drift affects the adaptive potential. I will discuss the findings particularly in relation to the persistence of small, inbreeding populations of endangered species.

02-04 Talk

SURVIVAL OR EXTINCTION: HOW FAST CAN THE RED QUEEN RUN?

Leonard Nunney [1]

[1] *University of California, Riverside, Biology, 92521, Riverside, USA*

leonard.nunney@ucr.edu

Climate change is a major threat to biodiversity that is amplified by habitat loss and fragmentation limiting the ability of many species to shift their range. Range-bound species must adapt to climate change or face extinction. Simulations showed that long-term adaptation more than 10x faster than Haldane’s classic limit of 1 genetic substitution per 300 generations can be sustained, but it requires populations of about 10^5 or more. Conservation plans for range-bound species should recognize that small populations (of order 10^3 or less) are likely to have maximum sustainable rates of adaptation slower than Haldane’s rate, severely limiting their long-term response to rapid climate change. However, simulations showed that linking small populations by dispersal exceeding about two effective migrants per generation creates a metapopulation capable of adapting as an integrated unit. These results argue for significant investment in wildlife corridors, carefully designed to ensure effective function.

02-05 Talk

POPULATION RESPONSES TO INBREEDING AND ENVIRONMENTAL PERTURBATIONS: AN EXPERIMENTAL STUDY.

Audrey Zannese [1], Steve M. Sait [1], Tim G. Benton [1]

[1] *University of Leeds, Institute of Integrative and Comparative Biology, LS2 9JT, Leeds, UK*

bgyaz@leeds.ac.uk

To understand how populations respond to environmental stress and genetic deterioration is of crucial importance for their management. Many studies have shown the impact of either environmental factors or genetic factors on the extinction of small populations, yet few studies have investigated the long-term dynamics of populations subject to both factors.

From this motivation, we conducted an experiment using a soil mite to explore how environmental perturbations and loss of genetic diversity interact to affect the dynamics of populations.

We present the results of this experiment explaining the differences in dynamics as a function of the various treatments the populations were subjected to, loss of genetic diversity and changes in life-history traits.

02-06 Talk

THE EVOLUTION OF INBREEDING DEPRESSION IN A METAPOPULATION

Shu-Rong Zhou [1], John R. Pannell [1]

[1] *University of Oxford, Department of Plant Sciences, South Parks Road, OX1 3RB, Oxford, UK*

shurong.zhou@plants.ox.ac.uk

There has been much recent interest in the effects of metapopulation processes on the evolution of inbreeding depression. However, no study has yet considered how the colonisation-extinction dynamics should affect the maintenance of variation at multiple loci that cause inbreeding depression in a metapopulation. In this paper, we present a metapopulation model to fill this gap. In particular, we summarise multi-locus, multi-demic simulations in which genetic variation causing inbreeding depression is maintained in a balance between deleterious mutations, selection, migration and drift; inbreeding depression is assessed at the local and metapopulation levels. Our results highlight the limitations of previous analytic predictions of inbreeding depression in a metapopulation that assume low mutation rates at single loci and low selection coefficients. We also extend earlier models by explicitly considering population turnover, thereby incorporating complications of recurrent local bottlenecks during colonisation and their interactions with migration. We discuss the implications of our results for the demographic and genetic viability of populations subject to colonisation and extinction dynamics.

02-07 Talk

INBREEDING AND ENVIRONMENTAL STRESS – INVESTIGATED ON DIFFERENT LEVELS OF BIOLOGICAL ORGANIZATION USING DROSOPHILA AS A MODEL ORGANISM

Torsten N. Kristensen [1]

[1] *Aarhus University, Biology and Genetics and Biotechnology, Blichers Allé 20, P.O. BOX 50, DK-8830, Tjele, Denmark*

torsten.nygaard@agrsci.dk

Increased rates of inbreeding due to reduced population size are often observed in small populations in the wild and in captive populations of zoo and livestock animals. We investigate the impact of inbreeding on fitness and genetic variance. 'Omics' technologies can be used to reveal new information on the impact of inbreeding on different levels of biological organization. Results from our lab suggest that inbreeding leads to marked changes in gene expression, proteome and metabolomic profiles and that inbreeding and environmental stress both independently and synergistically affect these traits. Fitness consequences of inbreeding seem to be line, environment and trait specific. To increase our knowledge on the environmental impact of inbreeding depression we have recently estimated fitness components in the field in inbred and outbred populations. Apart from affecting the mean of traits population sizes also impact on the additive genetic variance. Some of our recent results suggest that population bottlenecks - contrary to neutral expectations - may lead to an increase in additive genetic variance in a restricted species of *Drosophila* known to have low evolutionary potential for desiccation resistance.

02-08 Talk

PROTEOME SIGNATURES OF INBREEDING AND HEAT STRESS IN DROSOPHILA MELANOGASTER

Kamilla S. Pedersen [1, 2], Emøke Bendixen [3], Peer Berg [1], Torsten N. Kristensen [1, 2], Volker Loeschcke [2]

[1] *University of Aarhus, Genetics and Biotechnology, Blichersalle, 8830, Tjele, Denmark*
[2] *University of Aarhus, Ecology and Genetics, Ny Munkegade, 8000, Aarhus, Denmark*
[3] *University of Aarhus, Animal Health, Welfare and Nutrition, Blichersalle, 8830, Tjele, Denmark*

kamillas.pedersen@agrsci.dk

The deleterious consequences of inbreeding, especially on fitness traits are well established, but the underlying mechanisms are not yet thoroughly understood. This project aims at contributing with knowledge on the effects of inbreeding at the proteome. We performed a proteome analysis on replicate inbred ($F = 0.67$) and outbred lines of male *Drosophila melanogaster*, exposed to benign or stressful conditions (high temperature). To assess global proteome changes we used a robust shotgun proteomic approach (2D-LC-MS/MS). For quantitation of up- and down-regulated proteins, isobaric tags for relative and absolute quantitation (iTRAQ) were employed. Results indicate that the effect of inbreeding and heat stress can be detected at the proteome level. We were able to identify and quantify approximately 600 proteins whereof several proteins were differentially expressed in inbred and outbred *D. melanogaster*. Proteome data will be discussed in relation to gene expression data and metabolite profiles from the same inbred and outbred *D. melanogaster* lines.

02-09 Talk

INBREEDING INCREASES RESTING METABOLIC RATE AND REDUCES ENERGY AVAILABLE FOR ALLOCATION

Tarmo Ketola [1], Janne Kotiaho [1]

[1] *University of Jyväskylä, Department of Biological and Environmental Science, Jyväskylä, Finland*

tketola@cc.jyu.fi

The amount of energy that an individual can utilize for various tasks is suggested to play predominant role in adaptation to changing environments. Therefore, traits that contribute to this "allocation ability" might be under strong selection. We tested the fitness role of metabolic traits that affect energy allocation ability, by inbreeding Gryllodes sigillatus crickets to a varying degree. From these crickets, we measured metabolic rates during activity, and at rest. We found that resting metabolic rate (ml $CO_2{}^{-h}$) rose due to inbreeding. In addition, total energy budget (ml CO_2), measured by forced exercise until exhaustion, remained fairly constant, or if anything, it tended to be reduced by inbreeding. These results are against the common expectation that high resting metabolic rates allow higher allocation ability. Our results suggest the opposite, as inbreeding, by increasing maintenance costs and lowering total energy budget, reduced allocation ability. This might limit the ability to adapt to changing environments by means of energy allocation.

02-10 Talk

INBREEDING-BY-ENVIRONMENT INTERACTIONS IN A WILD BIRD POPULATION

Marta Szulkin [1], Ben C. Sheldon [1]

[1] *University of Oxford, Department of Zoology, South Parks Road, OX1 3PS, Oxford, United Kingdom*

marta.szulkin@zoo.ox.ac.uk

It is often asserted that inbreeding depression can be environment-dependent: this may have important implications for the conservation and persistence of small populations. However, evidence for inbreeding-by-environment interactions from wild populations is scant, and often inconclusive. We used 41 years of breeding events to study inbreeding by environment (I × E) interactions in a wild great tit (*Parus major*) population. We investigated 11 measures of the environment to categorise environments as relatively good or poor, testing whether these measures influenced inbreeding depression. Although inbreeding always, and environmental quality often, significantly affected reproductive success, there was little evidence for statistically significant I × E interactions at the level of individual analyses. However, point estimates of the effect of the environment on inbreeding depression were sometimes considerable, and we show that the magnitude of the I × E interaction across environments is consistent with the expectation that this interaction is more marked across environmental axes with a closer link to overall fitness, with inbreeding depression being elevated under such conditions. Hence, our analyses provide evidence for an environmental dependence of the inbreeding × environment interaction: effectively an I × E × E. Overall, our analyses suggest that I x E interactions may be substantial in wild populations, although their detection for single traits may require very large samples, or high rates of inbreeding.

02-11 Talk

THE MAGNITUDE OF INBREEDING DEPRESSION DECREASES WITH ENVIRONMENTAL STRESS AS FEMALE COLLARED FLYCATCHERS CHANGE THEIR REPRODUCTIVE STRATEGY

Mårten B. Hjernquist [1]

[1] *Animal ecology/IEE, EBC, Uppsala University, Norbyv. 18D, 75236, Uppsala, Sweden*

marten.hjernquist@ebc.uu.se

The magnitude of inbreeding depression in both animals and plants increases with environmental stress. However, in the collared flycatcher (Ficedula albicollis) the negative effects of inbreeding decreases when they are nesting in poor quality territories, i.e. more stressful environments. Such contradicting relationships of inbreeding by environmental interactions can be explained with a change in female reproductive strategy in relation to the quality of her nest territory. Females in good territories are faithful to their partner whereas females in poor quality territories more often engage in extra pair copulations. Thus, the context dependent reproductive strategy of females will indirectly work as an inbreeding avoidance mechanism in stressful environments but not in good environments.

02-12 Talk

HETEROZYGOSITY-FITNESS CORRELATIONS IN A BOTTLENECKED ISLAND SPECIES; A CASE STUDY ON THE SEYCHELLES WARBLER

Lyanne Brouwer [1], Jan Komdeur [1], David S. Richardson [2]

[1] *University of Groningen, Animal Ecology Group, Kerklaan 30, 9750AA, Haren, Netherlands*
[2] *University of East Anglia, Centre for Ecology, Evolution and Conservation, NR4 7TJ, Norwich, England*

lyannebrouwer@hotmail.com

We used capture-recapture models to investigate the effects of both individual and parental heterozygosity on the survival of Seychelles warblers *(Acrocephalus sechellensis)*, an endemic island species which went through a severe population bottleneck in the middle of the last century. We found that an individual's survival was not correlated with multi-locus heterozygosity, or with heterozygosity at any specific locus. However, maternal, but not paternal, multi-locus heterozygosity was positively associated with offspring survival, but only in years with low survival probabilities. Heterozygosity-fitness correlations at microsatellite markers were generally assumed to reflect genome-wide effects. Although this might be true in partially inbred populations, such correlations may also arise as a result of local effects with specific markers being closely linked to genes which determine fitness. However, heterozygosities at the individual microsatellite loci were not correlated and therefore do not seem to reflect genome-wide heterozygosity. This suggests that even in a small bottlenecked population heterozygosity-fitness correlations may not be caused by genome-wide effects. Support for the local effects hypothesis was also equivocal; although three specific loci were associated with offspring survival, including all single locus heterozygosities as independent predictors for the variation in survival was not supported by the data. Investigating the relation between survival and heterozygosity at the MHC, a group of genes that play an important role in the immune system, will show whether more heterozygous individuals have an advantage as they should be able to detect and combat a wider range of pathogens than homozygotes. This could then explain why genetic variation at the MHC is maintained in this bottlenecked species.

02-13 Talk

GENETIC HISTORY, HABITAT QUALITY AND PAST SELECTION AS DETERMINANTS OF INBREEDING AND OUTBREEDING DEPRESSION IN HERBIVORE RESISTANCE AND FITNESS OF FRAGMENTED PLANT POPULATIONS

Roosa Leimu [1]

[1] *University of Potsdam, Institute for Biochemistry and Biology, 14469, Maulbeerallee 1, Potsdam, Germany*

roosa.leimu@utu.fi

Habitat fragmentation reduces population size and increases isolation. Inbreeding often increases in small populations and can lead to inbreeding depression. Isolation can increase genetic differentiation between populations, which may disrupt co-adapted gene complexes and local adaptation if, inter-population crosses are conducted to reintroduce and restore for conservation purposes. Inbreeding and outbreeding depression are seldom constant across populations and rather vary depending on life-history stage, measured traits, abiotic and biotic environment and genetic history. How environmental and genetic factors interact to affect inbreeding and outbreeding depression is not clear and has not been addressed for interactions between plants and their natural enemies. This study examines the effects of genetic background, habitat quality and history of herbivory on inbreeding and outbreeding depression in herbivore resistance and fitness in 17 fragmented populations of the perennial herb, Lychnis flos-cuculi. Inbreeding depression in resistance was found in populations with higher past herbivory and lower levels of inbreeding. Outbreeding depression, in turn, was more sever for plants of small populations when crossed with plants from other populations of ecologically similar habitat. Outbreeding depression in resistance was greater for populations with less inbreeding. Inbreeding and outbreeding depression were further influenced by altitude and habitat quality. Herbivory altered the effects of inbreeding and among population outbreeding on plant fitness depending on genetic and ecological population traits. The results provide novel information on the effects of environmental and genetic factors on inbreeding and outbreeding depression, and on evolutionary consequences of habitat fragmentation on plant-herbivore interactions.

02-14 Talk

DECREASED PLANT VIABILITY DUE TO GENETIC EROSION IN A FRAGMENTED LANDSCAPE

Andrea R. Pluess [1], Jürg Stöcklin [2]

[1] *ETH, Swiss Federal Institute of Technology Zurich, Environmental Sciences, Universitaetstrasse 16, 8092, Zurich, Switzerland*
[2] *University of Basel, Environmental Sciences, Schoenbeinstrasse 6, 4056, Basel, Switzerland*

andrea.pluess@env.ethz.ch

Reduction and fragmentation of habitat might induce genetic erosion leading to impoverished genetic diversity and reduced fitness. Uncertainty as to the degree to which adaptive traits are reflected by neutral molecular diversity makes it imperative to study both. To test for genetic erosion in *Scabiosa columbaria* we combine molecular diversity with fitness-relevant phenotypic traits measured in a common garden in plants from eleven populations of different sizes.
Neutral molecular diversity within populations based on RAPD-PCR was variable and relatively high. Genetic diversity was not correlated with population size, but the smallest were the least diverse populations. Population differentiation was moderate ($G_{ST} = 0.12$) despite the spatial arrangement of the study populations within a relatively small area (37 x 11 km). In the common garden experiment, mean above-ground biomass was largely reduced when plants had to compete with *Bromus* irrespective of population origin. Mean fitness of populations decreased when molecular diversity was low in the competition treatment. Accordingly, the relative competition ability of *Scabiosa* plants decreased when molecular diversity was low. Moreover phenotypic plasticity decreased with decreasing molecular diversity.
Our results suggest an increased risk of local extinction of *S. columbaria* in the Swiss Jura caused by a decreased viability and reduced phenotypic plasticity due to genetic erosion in small populations. Restoration efforts should consider genetic diversity and should account for possible interactions between neutral genetic diversity and environmental variation on population viability.

02-01 Poster

INBREEDING AND INBREEDING DEPRESSION IN A SIBERIAN JAY POPULATION

Jussi S. Alho [1], Bo-Göran Lillandt [1], Juha Merilä [1]

[1] *University of Helsinki, Department of Biological and Environmental Sciences, PO Box 65, 00014, Helsinki, Finland*

jussi.alho@helsinki.fi

Habitat loss and degradation can contribute to population declines directly, by reducing population sizes, and indirectly, by the effects of reduced genetic variation and increased likelihood of inbreeding. The relative roles of these processes and their interactions have important implications for conservation. We quantified the prevalence of inbreeding and the magnitude of inbreeding depression in a Finnish Siberian jay (Perisoreus infaustus) population that has been under a long-term field study since 1974 and which during that time has experienced severe changes in its forest habitat. All individuals have been genotyped with microsatellite markers allowing us to assign parentage, construct a pedigree and calculate individual inbreeding coefficients. Subsequently, we estimated what the consequences of inbreeding have been at the population level.

02-02 Poster

QUANTITATIVE GENETIC EFFECTS OF BOTTLENECKS: EXPERIMENTAL EVIDENCE FROM A WILD PLANT SPECIES

Stefan Andersson [1], Maarten Ellmer [1], Tove H. Jörgensen [2], Anna Palmé [3]

[1] *Lund University, Ecology, Sölvegatan 37, 223 62, Lund, Sweden*
[2] *University of East Anglia, Ecology, Evolution and Conservation, NR4 7TJ, Norwich, United Kingdom*
[3] *Stockholm University, Zoology, 106 91, Stockholm, Sweden*

stefan.andersson@ekol.lu.se

Understanding the genetic consequences of changes in population size is fundamental in evolutionary biology, but also in applied fields such as conservation biology. In the study presented here, we have carried out a replicated experiment with the plant *Nigella degenii* to explore the quantitative genetic effects of a single-founder bottleneck, with special emphasis on the hierarchical partitioning of genetic variance and line-specific changes in the genetic (co)variance (G) matrix. Estimates of the within- and between-line genetic variance for a measure of flower size (sepal length), obtained four generations after the founder event, were in good agreement with predictions from additive neutral theory, whereas flowering date, flower number, plant stature and leaf length showed an excess of within-line genetic variance and a deficiency of between-line genetic variance. The latter discrepancies are consistent with bottleneck-induced conversion of nonadditive into additive genetic variance, but could also be a manifestation of selection, given the small fraction of lines (23%) that remained viable until the end of the experiment. The bottleneck caused stochastic, element-specific changes in the G matrix, and a resultant change in the principal component structure, rather than a proportional decline in all (co)variances. Thus, the predicted selection responses (estimated from the G matrices under two hypothetical selection regimes) were idiosyncratic, varying with the specific founder involved. Results of this experiment illustrate the potential for bottlenecks to alter the persistence of genetic constraints and the evolutionary lability of natural populations.

02-03 Poster

RAPID EVOLUTION AND HYBRIDIZATION IN DISTINCT SYMPATRIC WHITEFISH FORMS IN A SWISS LAKE

David Bittner [1], Laurent Excoffier [1], Carlo R. Largiader [2]

[1] *University of Berne, Computational and Molecular Population Genetics, Baltzerstrasse 6, 3012, Berne, Switzerlannd*
[2] *Inselspital University Hospital, Clinical Chemistry, Inselspital, 3010, Berne, Switzerlannd*

david.bittner@zoo.unibe.ch

Among all freshwater lake-dwelling fish of the northern hemisphere the genus *Coregonus* (whitefish) show exceptionally high levels of diversity with respect to the existence of multiple morphologically and ecologically distinct forms within and among lakes. These forms have been proposed having evolved independently in many postglacial lakes through rapid adaptive radiation. For Lake Thun, four genetically distinct whitefish forms have been described. In this study we focus on potential recent hybridization between the two unmanaged summer spawning forms, which has been suspected based on rapid temporal changes in an important adaptive morphological trait, i.e. the number of gill rakers, and recent observations of dramatic levels of gonad deformations among summer spawning forms. Genetic analysis based on eleven microsatellite loci of 282 adult individuals revealed significant genetic structuring among all known spawning sites of summer spawning forms, which could be explained by the presence of two populations occurring at different relative proportions on all seven sites. We found high correlation between gill raker numbers and multilocus genotypes indicating also a strong morphological differentiation in this highly heritable trait determining feeding spectrum (mean difference in gill raker counts ~ 15 units). Using Bayesian methods to infer individual admixture rates and detection of hybrid genotypes, we found indications of recent but limited hybridization, especially at one site. Furthermore, by comparing present with historical gill raker data, we found strong signals for rapid evolution (mean |haldane| = 0.22) through strong directional selection (mean |selection intensity| = 0.29) for this trait in both summer spawning populations. We hypothesize that the changes in gill raker counts reflect a response to changes in the tropic state of the lake, induced in the 1960ies.

02-04 Poster

LOCAL ADAPTATION AND CO-GRADIENT SELECTION IN THE ALPINE PLANT, POA HIEMATA, ALONG A NARROW ALTITUDINAL GRADIENT

Sean G. Byars [1], Ary A. Hoffmann [1]

[1] *The University of Melbourne, Genetics, Level 2, Bio 21 Institute, 30 Flemington Road, Parkville, 3010, Melbourne, Australia*

s.byars@pgrad.unimelb.edu.au

Alpine environments are particularly susceptible to environmental changes associated with global warming but there is potential for alpine plants to adapt to warming if local adaptation occurs and gene flow allows genotypes adapted to low altitude to colonize higher altitude sites. Here we examine the adaptive potential of a common alpine grass, *Poa hiemata*, within the restricted alpine habitat of Australian mountains, across a narrow altitudinal gradient replicated in three sites. Grasses at high altitude sites had shorter leaf lengths and larger circumferences than those at lower sites. Transplant experiments with clonal material and plants grown from seeds indicated that these differences were partly genetic, with environmental and genetic factors contributing roughly equally to the differences between altitudes. Differences in altitudinal forms were also evident in a common garden experiment. Plants showed a home-site advantage in terms of survival. Moreover, a fitness analysis indicated that at high altitude sites, selection was directed towards plants with short leaves and larger circumferences, whereas the opposite traits were favoured at the low altitude sites. These findings indicate cogradient selection and a substantial potential for both plastic and genotypic shifts in response to warming in *P. hiemata*.

02-05 Poster

GENETIC VARIABILITY COMPARISIONS BETWEEN THE EXTANT ENDANGERED EUROPEAN MINK (MUSTELA LUTREOLA) POPULATIONS

Maria Teresa Cabria [1], Elena G. Gonzalez [2], Benjamín J. Gómez-Moliner [1], Johan R. Michaux [3], Rafael Zardoya [4]

[1] Basque Country University, Zoology Department, Pharmacy Faculty, Paseo de la Universidad,7, 01006 Vitoria-Gasteiz, Spain
[2] National Museum Natural Sciences, José Gutiérrez Abascal, 2, 28006 Madrid, Spain
[3] International Agropolis de Baillarguet, Centre de Biologie et de Gestion des Populations, CS 30016, 34988 Montferrier-sur-Lez cedex, France
[4] 28006 Madrid, National Museum Natural Sciences, José Gutiérrez Abascal, 2, 28006 Madrid, Spain

maitec79@yahoo.es

The European mink (*Mustela lutreola*) is one of the European's most threatened carnivore species, listed as endangered in IUCN Red List (http://www.iucnredlist.org) due to a drastic population decline during the last century. The extant populations comprise three genetically distinct demes, Western (restricted to south-western France and northern Spain), South-eastern (limited to Romania) and North-eastern Europe (distributed into different parts of Estonia, Belarus and Russia). We assess levels and patterns of variation in both mitochondrial control region sequences and nuclear microsatellites to determine patterns of genetic diversity of the fragmented European mink populations, as well as to infer historical colonization and migrations patterns. Phylogenetic reconstructions and population genetic analyses revealed a moderately–high genetic diversity in the Eastern populations and subtle genetic substructure associated to different geographical regions and river basins. In contrast, the Western populations constitute a monophyletic group and showed a total absence of mtDNA control region sequence variation. Our results supported the hypothesis of a European re-colonization process from a single glacial refugee previously proposed by others authors. All this information will be useful in further management decisions and for improving the present conservation and monitoring breeding programs.

02-06 Poster

PHENOTYPIC AND GENETIC VARIABILITY IN DIFFERENT MORPHOLOGICAL TRAITS UNDER VARIOUS ENVIRONMENTAL STRESSES IN DROSOPHILA ANANASSAE

Chavali Vishalakshi [1], B N. Singh [1]

[1] Banaras Hindu Univeristy, Zoology, Genetics laboratory, Department of Zoology, Banaras Hindu University, 221005, Varanasi, India

vishalac_zoo@rediffmail.com

The diversity of life forms reflects the dynamic conflict between the organism and its environment. In the present study, we have investigated the effect of various environmental stresses (nutrition, temperature and larval crowding) on phenotypic and genetic variability and the levels of fluctuating asymmetry (FA) in different morphological traits (sternopleural bristle number, wing length, wing to thorax ratio, sex comb tooth number and ovariole number) in *Drosophila ananassae*. In the stressful conditions, the phenotypic and genetic variations are higher than in non stressful conditions for all the traits. Both the heritability and evolvability estimates were higher in the stressful conditions reflecting an apparent increase in the additive genetic variation under stress. The levels of FA wing length and sexual traits are higher than other morphological traits and the variability is more in males than in females. However, the results suggest that the effect of environmental stress appears to be trait and sex specific and this warns against the generalization about the behaviour of genetic and phenotypic variations under extreme environmental conditions and also for the use of FA as a bio indicator of environmental stress.

02-07 Poster

“WHERE’S MY MUMMY?” EVOLUTIONARY AND CONSERVATION IMPLICATIONS OF CALF SWAPPING IN THE WHITE RHINOCEROS

Natalie J. Coutts [1], Jacqueline M. Bishop [1], Janet L. Rachlow [2], Colleen O'Ryan [1]

[1] University of Cape Town, Molecular and Cellular Biology, Private Bag Rondebosch, 7700, Cape Town, South Africa
[2] University of Idaho, Fish and Wildlife Resources, ID 83844-1136, Moscow, United States of America

ncoutts@science.uct.ac.za

Sophisticated recognition mechanisms between parents and offspring are essential when parental investment is large and social organisation may lead to identification errors. Adaptations for mother-offspring recognition vary widely across taxa, directly influencing individual fitness by preventing costly maternal investment in offspring that are not their own. In this study we report the incidence of calf swapping among females in two isolated populations of southern white rhinoceroses (*Ceratotherium simum simum*). Persecution of rhinoceros species and resultant precipitous declines in population numbers has forced conservation to focus on establishing protected reserves and game parks. These approaches have enabled southern white rhino to recover from ~100 individuals at the beginning of the 20th century to ~11 500 individuals today. Ten microsatellite markers were analysed to assign parentage in two seeded populations, where field observations suggested the occurrence of calf swapping. Allelic mismatches at more than one locus were discovered in 6/20 maternal/offspring combinations in Welgevonden Reserve, South Africa, and 5/33 in Matobo National Park, Zimbabwe. This subspecies is characterised by low levels of genetic diversity (mean values of 2.63 alleles / locus and heterozygosity of 0.39) such that the genotypes of a number of adult females may match a particular calf; therefore these mismatches are noteworthy. Current unnaturally high population densities, resulting from restricted dispersal and high fecundity, necessitate management intervention. Historically, white rhino were naturally widely dispersed and we hypothesize that contemporary population densities contribute towards occurrences of calf swapping in extant populations.

02-08 Poster

SEX, GENOTYPIC DIVERSITY AND THE SURVIVAL OF PARTHENOGENETIC FLATWORM POPULATIONS

Thomas G. D'Souza [1], Nico K. Michiels [1]

[1] University Tuebingen, Animal Evolutionary Ecology, Auf der Morgenstelle 28, 72076, Tuebingen, Germany

thomas.dsouza@uni-tuebingen.de

One explanation for the success of sexual reproduction is that sex increases the efficacy of natural selection. Fusion of gametes and recombination lead to fitness variance among offspring which then offers a wider target for natural selection. Consequently, adaptation to changing environments is accelerated and population mean fitness will increase, which in turn decreases the likelihood of population extinction.

In the present study we investigated whether rare sex is accompanied by increase in variation and mean of fitness in natural subpopulations of parthenogenetic forms of the planarian flatworm *Schmidtea polychroa*. Parthenogenetic *S. polychroa* mainly reproduces clonally with occasional sexual reproduction leading to a substantial increase of genotypic diversity and telltale signatures in the population genetic structure. We correlated genotypic diversity, used as a reliable estimate for rare sex, with fitness attributes of six genetically differentiated locations within one meta-population. Results indicate strong, positive correlations of genotypic diversity with variance as well as with mean total offspring number produced during a five-week period.

We conclude that occasional sex and increased genotypic diversity facilitate adaptation to fluctuating environments and may therefore explain the survival and persistence of parthenogenetic populations.

02-09 Poster

ADAPTATION TO MULTIPLE STRESSORS THROUGH STRESS-SPECIFIC MECHANISMS IN NATURAL POPULATIONS

Agnieszka Doroszuk [1], Rebeca Garcia-Gallego [1], Jan Kammenga [1]

[1] *Wageningen University, Laboratory of Nematology, Binnenhaven 5, 6709 PD, Wageningen, The Netherlands*

agnieszka.doroszuk@wur.nl

Natural populations are often affected by multiple stressors, however little is known about their evolutionary responses in such environments. One of the most relevant questions is whether adaptations to multiple stressors arise through universal mechanisms promoting resistance for many stressors or are the consequence of stress-specific mechanisms. In our previous study, we showed that natural populations of the parthenogenetic nematode *Acrobeloides nanus* underwent adaptive divergence of life-history traits during 20 years of exposure to multiple-stress- (low pH, high copper concentration) and control treatments in an evolution experiment in the field. The populations from the multiple-stress treatment showed a higher resistance to both stresses. In this study, we investigated whether this pattern can be attributed to a general stress-resistance mechanism. For that purpose, we analysed evolutionary responses of the populations originating from the same experimental field from two single-stress treatments, namely, the low pH treatment and the high copper treatment. A reaction norm experiment indicated life-history adaptation of the nematodes from the high copper treatment to high copper concentrations. The increased copper tolerance in these populations was, however, not accompanied by the increased tolerance to low pH levels, as indicated by pH-response experiment. In a similar manner, the populations from the low pH treatment showed an adaptive response to low pH levels. Also in this case, the increased tolerance to low pH did not result in higher resistance to copper. These results indicate no apparent correlation between the resistance to copper and to low pH in *A. nanus*. Moreover, they suggest that the adaptation to the combination of stressors cannot be attributed to a single general stress resistance mechanism, but rather arose through two unrelated stress-specific mechanisms.

02-10 Poster

ANTHROPOGENIC ACTIVITIES AFFECT COLONY GENETIC STRUCTURE OF A SOIL-FEEDING TERMITE, LABIOTERMES LABRALIS (ISOPTERA : TERMITIDAE) FROM FRENCH GUIANA

Lise Dupont [1], Virginie Roy [2], Asmae Bakkali [1], Myriam Harry [1]

[1] *Université Paris 12, UMR137-BIOSOL-LBSE, 61 avn Général de Gaulle, 94010, Créteil cedex, France*
[2] *Université Paris 12, UMR137-BIOSOL-LEST, 61 avn Général de Gaulle, 94010, Créteil cedex, France*

lise.dupont@univ-paris12.fr

In tropical ecosystem, soil-feeding termites act as ecosystem-engineers, playing a fundamental role in soil structure and fertility. Because of their sensitivity to anthropogenic activities, soil-feeders may be used as bio-indicator of forest disturbance. One of the key determinants of genetic structure within social insect populations is the breeding system of social groups which defines the degree of relatedness between nestmates. Knowledge about breeding strategy in these species is thus fundamental to interpret modifications in population genetic structure in association with human activities. Breeding systems in termites may be of three kinds: monogamy, punctual polygamy and obligatory polygamy. Here, we used six microsatellite markers and parentage assignment method to investigate breeding mechanisms in colonies of the soil-feeding termite *Labiotermes labralis* (Termitidae), one of the most abundant termites in the Amazonian primary forest. Three sites from French Guiana presenting variable degree of forest degradation were studied. Parentage analysis revealed that the totality of the 18 nest (N = 20±1) showed pattern of genotypic frequencies consistent with their origin from a single mated pair indicating that monogamy is the general trend in *Labiotermes labralis*. In addition, a larger mean relatedness between nestmates was observed in colonies from the most disturbed habitat suggesting that human activities affect *L. labralis* colony genetic structure.

02-11 Poster

PHYLOGEOGRAPHY OF SCIURUS VULGARIS SUGGESTS ENDEMIC LINEAGE IN SOUTHERN ITALY (2ND SUITABLE SYMPOSIUM: INTEGRATING ECOLOGY & EVOLUTION

Andrea Grill [1], Giovanni Amori [1], Gaetano Aloise [1], Irene Lisi [1], Ferdinand Bego [1], Ettore Randi [1]

[1] *Istituto Nazionale per la Fauna Selvatica (INFS), Genetics Department, Via Cà Fornacetta 9, 40064, Ozzano Emilia (BO), Italy*

a.grill@tiscali.it

The red squirrel, *Sciurus vulgaris*, lives in conifer and broadleaf forests throughout Europe and Asia. It exhibits wide phenotypic variation in coat colors. A range of subspecies have been described, exclusively on the basis of morphological characters. Molecular phylogeographic data are scarce, despite the species' protection under the Bern Convention due to its dramatic decline in Europe. We sequenced parts of the mitochondrial DNA gene (*D-Loop*, 260bp, and *cytochrome b*, 500bp), as well as an intron of the nuclear gene *c-myc* (500bp) of *S. vulgaris* collected from Italy, Albania, Austria, Greece, Russia, Portugal, and Spain. Eight variable microsatellite loci were amplified for the same individuals. The analyses detected four main genetic lineages not corresponding to the described subspecies: a) an Alpine-Central European-Balkan group, b) an Iberian group, c) a Russian group, and d) a separate group of individuals collected in the southern-most part of the Italian peninsula (Calabria). The latter group is extremely differentiated, with genetic distances to Northern and Central Italian populations much greater than to the Russian or the Iberian ones in all studied genes. Separation of the Calabrian lineage happened at least 150,000 years before present, whereas the Alpine-Central-European group shows traces of a rapid population expansion about 40,000 years ago, following an expansion of forests during interglacial warming. An explanation for the surprising differentiation of the Calabrian squirrels might be a close association to their food plant, the endemic Calabrian pine tree, or isolation during glacial maxima. This endemic lineage forms a distinct Evolutionary Unit with an extremely low genetic diversity and its protection should be prioritized.

02-12 Poster

TWO-STEP MULTIPLEX PCR IMPROVES THE SPEED AND ACCURACY OF GENOTYPING USING PRIMATE FECAL DNA.

Mimi Arandjelovic [1], Katerina Guschanski [1], Grit Schubert [1], Tara R. Harris [1], Olaf Thalmann [1], Linda Vigilant [1]

[1] *Max Planck Institute for Evolutionary Anthropology, Primatology, Deutscher Platz 6, 04103, Leipzig, Germany*

guschanski@eva.mpg.de

Genetic studies of wild animal populations rely heavily on the genotyping of large numbers of non-invasively collected samples. However, extracts from such samples typically contain low quantities of DNA. Multiple PCR repetitions for each sample are required in order to overcome low amplification success rates and to avoid genotyping errors such as allelic dropout and false alleles.

Here we describe a two-step multiplexing PCR procedure that allows rapid genotyping using at least 20 different microsatellite loci. In the first step, all loci are pre-amplified simultaneously in a single pooled PCR containing all primers. In the second step, aliquots of the first reaction are re-amplified in locus-specific PCRs, each with a single primer pair. We tested this protocol using large numbers of samples from western chimpanzees, western gorillas, eastern gorillas as well as from black and white colobus monkeys. Although this sensitive approach required the establishment of stringent rules to avoid contamination, it worked well for extracts with low DNA quantities and had an overall higher PCR success rate. We observed lower dropout rates than when using a standard singleplex PCR approach, so that the number of PCR replications needed to reliably genotype each sample was greatly reduced. Use of the multiplex approach when genotyping large sets of noninvasive or standard samples should result in a considerable savings of time and materials.

02-13 Poster

POSTGLACIAL EXPANSION AND CURRENT FRAGMENTATION: MITOCHONDRIAL DNA AND MICROSATELLITE VARIATION IN THE EUROPEAN FIRE-BELLIED TOAD, BOMBINA BOMBINA, FROM THE NORTHERN EDGE OF ITS RANGE

J. Susanne Hauswaldt [1], Christiane Schroeder [2], Heiko Stuckas [3], Sebastian Lippold [3], Ralph Tiedemann [3]

[1] University of Cologne, Evolutionary Biology, Zuelpicher Str. 47, 50674, Cologne, Germany
[2] University of Potsdam, Evolutionary Biology/Systematic Zoology, Zuelpicher Str. 47, 50939, Potsdam, Germany
[3] University of Potsdam, Evolutionary Biology/Systematic Zoology, Karl-Liebknecht-Str. 24-25, 14476, Potsdam, Germany

shauswal@uni-koeln.de

The fire-bellied toad is among the most threatened species of amphibians in Europe. We have analyzed 21 populations of *Bombina bombina* from Denmark, Germany, Poland, and the Ukraine, of which many have undergone severe demographic changes over the last decades, for mtDNA control region haplotypes and 17 microsatellite loci. Despite low mitochondrial variability, the haplotype distribution pattern revealed a clear geographic pattern in concordance with the post-glacial expansion route. Microsatellite variation decreased drastically from central Europe towards the north. Even on a small geographic scale, we found significant genetic differentiation among populations: pairwise Fst values ranged from 0.05 to 0.55. Measures of genetic diversity (expected heterozygosity and allelic richness) were correlated with population size. Some populations showed signs of severe genetic bottlenecks. Genetic data also revealed allochtonous origin of several individuals from one of the sites in northern Germany. The results of this study are being used for management actions such as denomination of suitable source populations for release and translocation efforts.

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02-14 Poster

MULTILOCUS HETEROZYGOSITY AND INBREEDING DEPRESSION IN AN INSULAR HOUSE SPARROW METAPOPULATION

Henrik Jensen [1], Erlend Myre Bremset [1], Thor Harald Ringsby [1], Bernt-Erik Sæther [1]

[1] NTNU, Dept. of Biology, Realfagbygget, N-7491, Trondheim, Norway

Henrik.Jensen@bio.ntnu.no

Inbreeding causes reduction of genetic variability that may have severe fitness consequences. In spite of its potential huge impact on viability and evolutionary processes especially in small populations, quantitative demonstrations of genetic and demographic effects of inbreeding in natural populations are few.

Here we examine the relationship between individual inbreeding coefficients (F) and individual standardized multilocus heterozygosity (H) in an insular metapopulation of house sparrows (*Passer domesticus*) in northern Norway in order to evaluate whether H is a good predictor for F. We then relate variation in fitness (i.e. the probability of surviving from fledging to recruitment) to F and H, which enables us to examine whether inbreeding depression is associated with a reduction in genetic variability.

The average level of inbreeding in the house sparrow metapopulation was high, and there was large inter-individual variation in F. As expected, standardized multilocus heterozygosity decreased with the level of inbreeding. The probability of recruitment was significantly negatively related to F, and, accordingly, increased with H. However, H explained no significant additional variation in recruitment rate than was explained by F. This suggests that H is a good predictor for F in this metapopulation, and that an increase in F is likely to be associated with a general increase in the level of homozygosity on loci across the genome, which has severe fitness consequences.

02-15 Poster

EFFECT OF ENVIRONMENTAL POLLUTION ON INTERPOPULATION DIFFERENCES OF INVERSION POLYMORPHISM IN DROSOPHILA SUBOBSCURA

Bojan Kenig [1], Zorana Kurbalija [1], Tatjana Savic [1], Marina Stamenkovic-Radak [2], Marko Andjelkovic [2]

[1] *Institute for Biological Research, Bulevar despota Stefana 142, 11000, Belgrade, Serbia*
[2] *Faculty of Biology, 11000, Belgrade, Serbia*

scarab372001@yahoo.com

Drosophila subobscura has a very rich inversion polymorphism at all five acrocentric chromosomes. It shows significant interpopulation differences in variability associated, to a certain degree, with adaptation processes in natural habitats of this species.

Focusing on studying the genetic aspect of ecosystem disturbance, we analyzed inversion polymorphism of two populations of *D. subobscura,* from differently polluted habitats. One population was from the central, urban part of Belgrade, with very high concentration of heavy metals registered in the soil. Another population was sampled from the locality about 100 km far from Belgrade with low level of heavy metal concentration in the soil, thus, considered as relatively unpolluted ecosystem.

The analysis of inversion polymorphism of *D. subobscura* populations from two habitats showed significant differences in the frequencies of particular gene arrangements of A and O chromosomes and of karyotypic combinations on all four autosomes. In the population from urban locality higher level of heterozygosity and lower value for Index of Free Recombination is obtained. The attained quantitative and qualitative interpopulation differences point to their association with differences of heavy metal pollution levels to which populations of *D. subobscura* have been exposed.

02-16 Poster

GENETIC STRUCTURE OF BRYOPHYTE POPULATIONS IN DISTURBED AND NATURAL ECOSYSTEMS

Helena Korpelainen [1], Viivi Virtanen [1], Kirsi Kostamo [1], Hanna Karttunen [1], Maria Pietiläinen [1]

[1] *University of Helsinki, Department of Applied Biology, P.O. Box 27, FI-00014, Helsinki, Finland*

helena.korpelainen@helsinki.fi

Many plant species have declined as a result of human activities, such as habitat fragmentation and reduction, which have led to a decrease in population size and genetic diversity. Anthropogenic effects are generally most pronounced in urban ecosystems, where habitat fragmentation may be accompanied with major changes in the quality of the environment and possibly exposure to environmental contaminants. In the present study, we have investigated the population biological processes of bryophytes in urban or otherwise disturbed ecosystems and compared them to those in populations occurring in natural or semi-natural habitats in southern Finland. The research concentrates on three bryophyte species, the mosses *Pleurozium schreberi* and *Rhytidiadelphus squarrosus*, and the hepatic *Plagiochila asplenioides*, which are all common taxa and known to occur also in human-impacted habitats. The general aim of the project is to investigate population processes, including genetic diversity, demographic structure and the role of selection in the maintenance of adaptive variation, and to find the causes influencing the performance of bryophyte populations occupying disturbed ecosystems when compared to populations inhabiting natural habitats. Here we report the results obtained from genetic assays conducted using microsatellite markers, which are usually considered neutral and which generally possess considerable variation. For each species we have developed 9-12 microsatellite markers which have now been analysed in the targeted populations. Most marker loci showed polymorphism at the within-population level. The amount of gene flow was considerable except in *R. squarrosus*, which commonly occurs in human-impacted sites and in which a population age effect on genetic diversity was detected. The population genetic characterization with the use of neutral marker loci forms a basis for the further analysis concentrating on the adaptive, gene-targeted variation in order to obtain information on functional variation and selection processes.

02-17 Poster

THE EFFECTS OF SEXUAL SELECTION AND INBREEDING ON LIFE HISTORY TRAITS IN THE GUPPY (POECILIA RETICULATA).

Line K. Larsen [1], Gunilla Rosenqvist [1], Christophe Pelabon [1]

[1] *NTNU, Department of biology, Høgskoleringen 5, Realfagbygget, 7491, Trondheim, Norway*

linekris@bio.ntnu.no

Guppies originally collected from the Quare River in Trinidad have been bred in captivity since 1998, today yielding 10 generation.

By separating them into 3 different breeding regimes we aimed to investigate the effects of inbreeding and sexual selection on fecundity related life history traits. The treatments are:

1. Mating by sexual selection. This treatment has the option of mate choice and mate competition, and a moderate level of inbreeding.
2. Outbreeding. Individuals who are least related are mated to each other. This treatment results in low inbreeding and no sexual selection.
3. Random mating. The female and male are chosen at random and mated. This treatment results in no sexual selection and has high levels of inbreeding.

Variables measured are clutch size, size of young at birth and age as well as size of males at maturation.

We expect to find a lower rate of fecundity and a later age of maturation in the inbred treatment and we expect sexual selection to have a positive effect on fecundity and also result in an earlier age at maturation.

02-18 Poster

ESTIMATING THE DISTRIBUTION OF MUTATIONAL EFFECTS

Laurence Loewe [1], Brian Charlesworth [1]

[1] *University of Edinburgh, Institute of Evolutionary Biology - School of Biological Sciences, Ashworth Laboratories - Kings Buildings - West Mains Road - Edinburgh EH9 3JT, Scotland UK*

Laurence.Loewe@ed.ac.uk

The properties of the distribution of deleterious mutational effects on fitness (DDME) are of fundamental importance for evolutionary genetics in general and for conservation genetics in particular. Since it is extremely difficult to determine the nature of this distribution, several methods using various assumptions about the DDME have been developed, for the purpose of parameter estimation. We apply a newly developed method to DNA sequence polymorphism data from two Drosophila species, and compare estimates of the parameters of the distribution of the heterozygous fitness effects of amino-acid mutations for several different distribution functions. The results exclude normal and gamma distributions, since these predict too few effectively lethal mutations, and power-law distributions because they predict too many lethals. Only the lognormal distribution appears to fit both the diversity data and the frequency of lethals. This DDME arises naturally in complex systems when independent factors contribute multiplicatively to an increase in fitness-reducing damage. Several important parameters, such as the fraction of effectively neutral non-synonymous mutations and the harmonic mean of non-neutral selection coefficients, are robust to the form of the DDME. Our results suggest that the DDME is very wide on a log scale, i.e. it encompasses selection coefficients from many orders of mangitude.

02-19 Poster

BACKGROUND SELECTION IN SINGLE GENES

Laurence Loewe [1], Brian Charlesworth [1]

[1] *University of Edinburgh, Institute of Evolutionary Biology - School of Biological Sciences, Ashworth Laboratories - Kings Buildings - West Mains Road - Edinburgh EH9 3JT, Scotland UK*

Laurence.Loewe@ed.ac.uk

Background selection involves the reduction in effective population size (Ne) caused by the removal of recurrent deleterious mutations from a population. Reductions in Ne are of interest for long-term conservation efforts, as they reduce the effectiveness of purifying selection and might hence accelerate deleterious mutation accumulation. Previous work has examined this process for large genomic regions. Here we focus on the level of a single gene or small group of genes, and investigate how the effects of background selection caused by nonsynonymous mutations are influenced by the lengths of coding sequences, the number and length of introns, intergenic distances, neighboring genes, mutation rate and recombination rate. We generate our predictions from estimates of the distribution of the fitness effects of nonsynonymous mutations, obtained from DNA sequence diversity data in Drosophila. Results for genes in regions with typical frequencies of crossing over in Drosophila melanogaster suggest that background selection may influence the effective population sizes of different regions of the same gene, consistent with observed differences in codon usage bias along genes. It may also help to cause the observed effects of gene length and introns on codon usage. Gene conversion plays a crucial role in determining the sizes of these effects. Results reveal the extraordinarily strong influence of the deleterious mutation rate on the strength of background selection. This has implications for conservation efforts of species in mutagenic habitats like some regenerated industrial wastelands.

02-20 Poster

ANALYSIS OF THE GENETIC STRUCTURE OF SCHREIBER´S GREEN LIZARD - CONSERVATION IMPLICATIONS FOR AN ENDEMIC SPECIES

Margarida C. Lopes [1], Vera L. Nunes [1], Francisco Pina-Martins [1], Manja U. Böhme [2], Thomas U. Berendonk [2], Nuno Ferrand [3], Octávio S. Paulo [1]

[1] *Faculdade de Ciências da Universidade de Lisboa, Department of Animal Biology, 1749-016 Lisboa, Portugal*
[2] *Univ. of Leipzig, Inst. Biology II, Dept. of Molecular Evolution & Animal Systematics, 04103, Leipzig, Germany*
[3] *Univ. do Porto, CIBIO, Campus Agrário de Vairão, 4485–661 Vairão, Portugal*

miclopes@gmail.com

The Quaternary Period is characterized by climatic oscillations which caused heavy changes in the demography and distribution of the endemic lizard *Lacerta schreiberi* in the Iberian Peninsula. The degree of population subdivision, gene flow among subpopulations, presence of secondary contact zones among different mitochondrial clades and the refuges' locations, were assessed analyzing 9 microsatellite loci of 627 individuals from 23 populations. Previously, mtDNA and PCR-RFLPs studies have revealed the existence of two main clades (A and B) within *L. schreiberi*, each one subdivided in two secondary clades (A_1, A_2, B_1 and B_2). The microsatellite analysis confirms genetic divergence between the two major clades and sub-clades due to restrict gene flow. Some admixture in the secondary contact zone across *Serra da Malcata* and *Serra da Gata* occur. A recent and probably anthropogenic effect has caused a fragmentation in the distribution thus generating low diversity within several isolated populations. It seems that *L. schreiberi* has survived in multiple and allopatric refugia within the main refugial areas with restricted gene flow among them. The establishment of ESUs (evolutionary significant unit) is recommended using Crandall and Bernatchez's suggestions. The genetic monitoring is crucial for the perseverance of this endemic species.

02-21 Poster

HIGH GENETIC DIVERSITY IN THE SNOWY OWL (*BUBO SCANDIACUS*)

Gunnhild Marthinsen [1], Liv Wennerberg [1], Roar Solheim [2], Jan T. Lifjeld [1]

[1] *University of Oslo, Natural History Museum, PO Box 1172 Blindern, 0318, Oslo, Norway*
[2] *Agder Museum of Natural History, Norway*

g.m.marthinsen@nhm.uio.no

The snowy owl (*Bubo scandiacus*) is a nomadic species with an Arctic circumpolar distribution. It has recently declined in the western Palearctic and may thus be worthy of special consideration for conservation. We have therefore investigated the level of gene flow, genetic structure and genetic diversity in three well separated geographic regions within the snowy owl's breeding range. We sequenced two mitochondrial genes; the control region and cytochrome *b*, and two Z-chromosome introns; VLDLR-9 and BRM□15. We found no phylogeographic structure, probably due to high levels of gene flow going on at present throughout its circumpolar range. A relatively high level of intra-population diversity compared to Scandinavian populations of three other owl species breeding in the temperate region was revealed. The long-term effective population size was estimated to 60 000 females (± 5 000, based on a 10% substitution rate per Myr for the control region, and two years generation time). We found signatures of a population expansion in a mismatch distribution analysis, however not corresponding to an exponential growth rate. Rather, a shifted peak in the mismatch distribution and a complex haplotype network with no central haplotype suggest that the snowy owl has been separated into several isolated populations and merged into panmictic groups several times. In the present panmictic population, the different haplotypes are intermingled and contribute to the high level of genetic diversity. The lack of phylogeographic structure is probably due to the snowy owl's capacity for long distance movements and its opportunistic breeding behaviour.

02-22 Poster

MTDNA VARIATION IN PERIPHERAL POPULATIONS OF THE GROUNDWATER AMPHIPOD GENUS *NIPHARGUS* (AMPHIPODA, CRUSTACEA) FROM THE MEUSE VALLEY (BELGIUM)

Severine Matthijs [1], Thierry Backeljau [1, 2], Frank Fiers [1]

[1] *Royal Belgian Institute of Natural Sciences, Vautierstraat 29, 1000, Brussels, Belgium*
[2] *University of Antwerp, Evolutionary Biology Group, Groenenborgerlaan 171, 2020, Antwerp, Belgium*

severine_matthijs@yahoo.com

Niphargus Schiödte, 1849 is a subterranean amphipod genus that occurs in groundwater habitats throughout Central and Southern Europe (with the exception of almost the entire Iberian peninsula). The animals can be caught in caves, wells and sources. Six *Niphargus* species occur in Belgium, where they represent peripheral populations, living close to the north to north-western border of their distribution. Peripheral populations often show a decrease in genetic diversity relative to central populations, from which they may be more or less isolated and hence differentiated. Peripheral populations may also be subject to different selection pressures, possibly reinforcing genetic differentiation and in some cases even speciation. In this context, the present study uses mtDNA sequence comparisons to investigate to what extent Belgian *Niphargus* sp. are genetically comparable and/or differentiated from populations elsewhere in Europe. In this way, we also try to assess the conservation value of the Belgian populations and to uncover eventual cryptic diversity. Local small scale population structuring will be studied by screening microsatellite and/or AFLP variation. Populations are being sampled in three areas around the river Meuse. Several sets of primers were tested for the mitochondrial gene fragments cytochrome oxidase c subunit I (COI), cytochrome B (cytB), 12S rDNA and 16S rDNA. Preliminary results show a considerable amount of variation for two of the studied species, *N. schellenbergi* and *N. kochianus dimorphopus*, and a rather low variation in a third species, *N. fontanus*. In the most 'variable' species, *N. k. dimorphopus*, there also seems to be some morphological variation, which may suggest that this might in fact be two species. In order to interpret the variation in Belgian *Niphargus* species, we aim to compare them with populations from elsewhere in Europe.

02-23 Poster

PALEOGENETICS AND PALEOLIMNOLOGY: TRACING PAST POPULATION-GENETIC CHANGES USING ANCIENT DNA RETRIEVED FROM PLANKTON REMAINS

Joachim Mergeay [1], Dirk Verschuren [2], Luc De Meester [1]

[1] *KULeuven, Lab. of Aquatic Ecology, Charles Deberiotstraat 32, 3000, Leuven, Belgium*
[2] *UGent, Biology - Limnology Unit, KL Ledeganckstraat 35, 9000, Ghent, Belgium*

joachim.mergeay@bio.kuleuven.be

Paleogenetics is the study of ancient DNA. When applied to natural ecological archives like lake sediments, it can open new doors in evolutionary biology by allowing one to track genetic changes in natural populations through time, and on very long time series. Water fleas such as *Daphnia* produce during their life cycle resistant dormant eggs encased in a rigid capsule (ephippium). When buried in lake sediments these eggs can remain viable for decades (up to at least 100 years). The DNA contained in dormant eggs is moreover protected against progressive degradation, even when the eggs are no longer viable. DNA extracted from dormant eggs of various ages can be used to investigate past population-genetic changes in response to specific events of natural environmental change or anthropogenic stress. We present three case studies on paleogenetics of *Daphnia*: (1) contrasting neutral genetic markers with ecologically relevant traits in a dynamic environment, (2) assessing the importance of old dormant eggs in population recovery after extinction, and (3) using paleogenetics in invasion biology and dynamics.

02-24 Poster

GENETIC CONSEQUENCES OF DECREASING POPULATION SIZE IN THE SELF-INCOMPATIBLE BRASSICA INSULARIS, WHAT FUTURE FOR THESE POPULATIONS?

Agnes Mignot [1], Sylvain Glemin [2]

[1] *Université Montpellier 2 / Institut des Sciences de l'Evolution, Genetique et Environnement, cc065, place E. Bataillon, 34095, Montpellier, France*
[2] *Université Montpellier 2 / Institut des Sciences de l'Evolution, Phylogénie Moléculaire, cc063, place E. Bataillon, 34095, Montpellier, France*

agnes.mignot@univ-montp2.fr

Self-incompatibility (SI) systems are both widespread elements of plant reproductive systems and essential for the genetic diversity of many species. They indeed enforce outcrossing and thus help maintain genetic exchange within and between populations. In general, numerous S-alleles are maintained by negative frequency-dependent selection in the same population, allowing most crosses between individuals to be compatible. In small populations of endangered plants however, the number of S-alleles is reduced, which can limit mate availability and reduce fecundity. Despite increasing evidence for the negative effect of self-incompatibility in small populations, few studies have focused on their functioning within natural populations and on their demographic and evolutionary consequences. In *Brassica insularis*, a rare self-incompatible species with small populations in Corsica, we studied the consequences of population size on both the number of S alleles and the reproductive output. The future of the smallest population at least is unambiguous: very low S-alleles number and mate availability do affect fecundity and threaten this population.

The survival success of declining populations with low S-alleles diversity is expected to depend heavily either on dispersal ability and successful immigration of new individuals/alleles or on the breakdown of the self-incompatibility system. We studied this latter alternative in *Brassica insularis*, with a particular focus on the level of inbreeding depression in these populations.

02-25 Poster

SEARCHING GENES WITH ADAPTIVE IMPORTANCE IN OCELLATED LIZARDS (LACERTA LEPIDA) FROM IBERIAN PENINSULA

Vera L. Nunes [1], Mark A. Beaumont [2], Roger K. Butlin [3], Octávio S. Paulo [1]

[1] *Faculdade de Ciências da Universidade de Lisboa, Department of Animal Biology, 1749-016, Lisboa, Portugal*
[2] *University of Reading, School of Animal and Microbial Sciences, P.O. Box 228, RG6 6AJ, Reading, UK*
[3] *University of Sheffield, Department of Animal and Plant Sciences, Sheffield S10 2TN, S Yorkshire England*

veralmn@sapo.pt

Identification of loci with adaptive importance is a relevant issue for conservation, since those loci are linked to phenotypic variation that confers increased fitness to different environments. The aim of this study is to identify genes under selection from a genome scan with AFLP markers. For this purpose, 12 populations of Ocellated lizard (*Lacerta lepida*) were selected from the Iberian Peninsula, with previously described morphological and genetic heterogeneity, including two recognized subspecies *L. lepida iberica* and *L. lepida nevadensis*. Variation in some morphological traits between those subspecies could be correlated with their local adaptation and is maintained by reduced gene flow, as suggested by the high levels of mitochondrial cytochrome *b* divergence. In order to identify loci responsible for those adaptive differences, two recent statistical approaches were applied to the obtained AFLP dataset, allowing detection of outlier frequencies that differ from neutral expectations. The generated data is also relevant for a better understanding of the speciation process underlying *L. lepida* population's divergence and their implications in future conservation management units' delimitation.

02-26 Poster

FISHERY-INDUCED DECREASE IN INDIVIDUAL GROWTH RATES: DISENTANGLING GENETIC FROM ENVIRONMENTAL EFFECTS

Sebastien Nussle [1], Claus Wedekind [1]

[1] *University of Lausanne, Department of Ecology and Evolution, Biophore, 1015, Lausanne, Switzerland*

sebastien.nussle@unil.ch

Theory predicts that certain kinds of size-selective fishing select against fast-growing genotypes and thereby change the genetics of wild populations. We analysed a 25-year monitoring survey on a population of Alpine whitefish (Coregonus lavaretus). Individual growth was determined from annuli on scales and compared to changes in the population's environment (lake temperatures, phosphorus concentration, algae growth). We found that about a fourth of the total decrease in individual growth rates may be linked to fishery-induced genetic changes. This suggests that size-selective fishing induces rapid evolution, and that the genetic consequences of fishing may be more important than previously thought.

02-27 Poster

INTERACTION BETWEEN ENVIRONMENTAL HETEROGENEITY, GENE FLOW AND INBREEDING DEPRESSION ON THE BUILDING OF SPATIAL GENETIC STRUCTURE

Sylvie Oddou-Muratorio [1], Francois Lefevre [1], Mariane Alleaume-Benharira [1]

[1] *URFM, INRA, F84000, Avignon, FRANCE*

oddou@avignon.inra.fr

In general, environmental conditions are not strictly homogenous in space and selection, e.g. for a stress, acts locally. For example, in Mediterranean plant populations it is well known that soil depth can vary tremendously on a small scale and it will determine the local intensity of drought stress. In such populations, the scale of environmental heterogeneity versus that of gene flow will thus strongly affect the spatial structure of genetic diversity. In this study, we used a spatially explicit model to investigate the interaction between environmental heterogeneity, gene flow and inbreeding depression in the building of spatial genetic structure within a continuous population.

Our model links genetic processes (mating system and inbreeding) and ecological processes (dispersal, growth, mortality) in a demographic, individual-based framework. It was calibrated on a model situation of an exotic forest tree species, *Cedrus atlantica*, that was introduced in South East of France mid XIXs. and expanded through natural regeneration since then. We studied in which conditions seed/pollen dispersal interact with environmental spatial heterogeneity for selection against inbred individuals, and discuss the consequences of these interactions for the evolutionary trajectory of this managed species.

02-28 Poster

ADAPTABILITY IN A GENETICALLY IMPOVERISHED AMPHIBIAN METAPOPULATION

Germán Orizaola [1], Anssi Laurila [1]

[1] *Uppsala University, Dept. Ecology and Evolution, Evolutionary Biology Center, Norbyvägen 18D, 75236, Uppsala, Sweden*

german.orizaola@ebc.uu.se

The adaptive potential of a population determines its possibilities to respond to environmental changes. Theory predicts reduced genetic diversity in small populations, partially due to higher allelic loss associated with genetic drift the smaller the population is. Therefore, small and isolated populations are exposed to a higher risk of extinction due their lower capacity to face environmental changes. Here, we examine the adaptability of a small and isolated population of the pool frog (*Rana lessonae*), harbouring very low molecular genetic variation. First, we analyse population differentiation in quantitative traits, comparing the results with those from a widespread species with ample genetic variation (moor frog, *Rana arvalis*). We detect higher population differentiation in *R. lessonae*, than in *R. arvalis* (overall Q_{ST}= 0.57 and 0.20 respectively). We also examine population differentiation and heritability of plastic responses to temperature variation in *R. lessonae*. Populations differ in both trait mean values and in the plastic responses, with higher plasticity in populations more exposed to temperature variation. Finally, we study climatic adaptation in *R. lessonae*, checking the effects of temperature variation on larval development in several populations around the Baltic. Higher growth rates were found for Swedish frogs when compared to Southern Baltic ones (Poland and Latvia), revealing adaptation to colder temperatures. Overall, the adaptability of Swedish pool frogs seems to be good, strong among-population variation in larval traits and trait plasticity existing at relatively small scale, and populations being adapted to local climate. These facts suggest higher evolutionary potential in this population, despite the very low molecular genetic variability.

02-29 Poster

GENETIC STRUCTURE OF THE EUROPEAN SPINY LOBSTER (PALINURUS ELEPHAS) FROM MEDITERRANEAN AND ATLANTIC WATERS

Ferran Palero [1], Pere Abello [2], Enrique MacPherson [3], Michele Gristina [4], Marta Pascual [1]

[1] *UNIVERSITY OF BARCELONA, GENETICS, AV. DIAGONAL, 645, 08028, BARCELONA, SPAIN*
[2] *ICM-CSIC, Passeig Marítim de la Barceloneta 37-49, 08003, BARCELONA, SPAIN*
[3] *CEAB-CSIC, Carrer d'Accés a la Cala Sant Francesc 14, 17300, BLANES, SPAIN*
[4] *IAMC-CNR, Via Luigi Vaccara, 61, 91026, MAZARA DEL VALLO, ITALY*

ferranpalero@ub.edu

The population genetic structure and distribution of a species are shaped by both past and present ecological processes acting on populations, such as recent paleoecological events (e.g., glaciations) and current pressures (e.g., over-exploitation, habitat degradation, introduction of invasive species). To investigate population structure in the European spiny lobster (*Palinurus elephas*) a portion of the COI gene was sequenced in 227 individuals from 11 localities, covering most of the present distribution of the species. A pattern of isolation by distance was found: increasing geographic distance is related to increasing genetic differentiation between populations. Divergence was found between Atlantic and Mediterranean regions, which could be explained by restricted gene flow between populations. These results reveal a possible reduction in the dispersal capability of the phyllosoma with respect to expected levels, given its long duration. Moreover, high variability was found in *P. elephas* populations, with the presence of one abundant haplotype and a large number of closely related haplotypes. This pattern indicates demographic changes, with a bottleneck and a recent expansion. Climatic fluctuations related to glacial cycles seem to have caused the present level of variability and nucleotide diversity found in the mtDNA of *P. elephas*. Therefore, past events have had a strong influence on the present population genetic structure, although the molecular marker also allowed us to detect genetic structuring caused by current factors.

02-30 Poster

ENVIRONMENTAL CHANGE, BODY SIZE VARIABILITY AND DEVELOPMENTAL STABILITY IN DROSOPHILA SUBOBSCURA

Aleksandra Patenkovic [1], Tatjana Savic [1], Marina Stamenkovic - Radak [2], Marko Andjelkovic [2]

[1] *Institute for Biological Research, Bulevar despota Stefana 142, 11000, Belgrade, Serbia*
[2] *Faculty of Biology, Studentski trg 3, 11000, Belgrade, Serbia*

aleksandra@ibiss.bg.ac.yu

The purpose of this study was to test whether genotypic differences of allozyme variants, under different environmental conditions, affect body size and developmental stability in *Drosophila subobscura*. In *Drosophila*, expression of amylase is affected by environmental conditions and components of the nutritional substrate, i.e. starch concentration. Discrete or abrupt changes in the composition of substrate on which flies develop and feed present environmental stress to which genotypes may respond differently through phenotypic variability**.** Wing length and width, and their fluctuating asymmetry (FA) as a measurement of developmental stability were assesed in both sexes of D.subobscura homozygous for AmyS or AmyF allele.

Body size was significantly increased on all starch concentrations if compared to the control substrate. Sex had no effect on the variability of developmental stability, regardless of genotype or substrate composition**.** Wing length shows significant FA variability under environmental change, and developmental stability of wing width depends of genotype. Genetic mechanisms leading to adaptation of a population to particular stressful conditions are possibly specific under given experimental circumstances and the response to stress is genotype and trait specific.

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02-31 Poster

INFLUENCE OF HUNTING PRESSURE ON POPULATION GENETIC STRUCTURE IN WILLOW GROUSE, LAGOPUS LAGOPUS, ASSESSED BY SNP MARKERS

María Quintela [1], Sofia Berlin [2], Jacob Höglund [1]

[1] *Uppsala University, Population Biology and Conservation Biology, Norbyvägen 18 D, SE- 752 36, Uppsala, Sweden*
[2] *Uppsala University, Evolutionary Biology, Norbyvägen. 18 D, SE-752 36, Uppsala, Sweden*

maria.quintela@ebc.uu.se

Lagopus lagopus (willow grouse or willow ptarmigan) is a gamebird inhabiting mainly boreal forests and tundra across northern Eurasia, Alaska and northern Canada. This species is hunted in most of its range and the habitats of the British subspecies *scoticus* (red grouse) are intensively managed to produce high densities for sport hunting. Therefore, a better understanding of the effects of hunting and habitat alteration on population structure is needed in order to perform a suitable management of populations.

Some thirty individuals were collected from Sweden, Norway and Scotland (2 populations each) in a gradient of hunting pressure. The aims of this work were to assess genetic diversity, population genetic structure and to relate genetic structure to relative levels of hunting. SNP (Single Nucleotide Polymorphism) markers were the marker of choice because of their wide range of applications and its duality as neutral and adaptive markers. Twenty exon primers scattered across all chromosomes and designed for chicken were amplified and PCR products were sequenced producing 101 segregation sites. A large degree of structure was found among Scandinavia and Scotland (overall F_{ST} of 0.168) and 83% of the variation has kept within populations. Moreover, most of these exon primers were successfully amplified on some other eleven species of birds.

02-32 Poster

SIMULATION-BASED METHODS AND ANCIENT DNA REVEAL CRYPTIC POPULATION HISTORY

Uma Ramakrishnan [1], Kim O'Keefe [2], Elizabeth A. Hadly [2]

[1] *National Centre for Biological Sciences, GKVK Campus, 560065, Bangalore, India*
[2] *Stanford University, Biological Sciences, Department of Biological Sciences, 94305, Stanford, CA, USA*

uramakri@ncbs.res.in

Reconstruction of demographic history based on modern genetic data alone provides insight into the ‘average’ picture of change over time, thus leaving many population historic processes undetected, or cryptic. Temporal genetic data present an opportunity to reveal more complex population histories. All ancient DNA datasets analyzed so far consider impacts of changes in population size, but ignore possible impacts of gene flow or population structure. Using a serial coalescent-based approach, we develop statistical methods that model population structure in past populations. Further, we present analyses of temporal genetic data from four species (bison, adelie penguin, European brown bear and ground squirrel) based on models that allow for changes in population size and structure through time. Our analyses reveal that in some cases, models with population structure and changes in population structure better explain the genetic data compared to models that only includes changes in population size. We conclude that population genetic samples over large temporal and geographic scales, when analyzed using more complex population genetic models are critical to understand past population and species evolution and hence for predicting their future.

02-33 Poster

CHARACTERIZATION OF THE NW IBERIAN POPULATIONS OF THE LIZARD IBEROLACERTA MONTICOLA AS REVEALED BY GENETICS, MORPHOLOGY AND ECOLOGY

Nuria Remon [1], Marta Vila [1], Pedro Galan [2], Horacio Naveira [1]

[1] *University of Coruña, Biology Cell and Molecular, Campus da Zapateira, Facultad de Ciencias, E 15008, A Coruña, Spain*
[2] *University of Coruña, Ecology, Animal and Plant Biology, Campus da Zapateira, Facultad de Ciencias, E 15008, A Coruña, Spain*

nremon@udc.es

The Iberian rock lizard (*Iberolacerta monticola*) has gone extinct or severely declined in several low-altitude and isolated populations in NW Spain during the last three decades. In order to assess the conservation status of this species in this area, we recorded morpho- and ecological data of individuals from eleven localities. We screened the genetic variability of these specimens by combining nuclear microsatellites and mitochondrial markers. One particular population (Montes do Pindo, A Coruña, 100 km from the nearest population) was largely differentiated from the others in the 450 bp of the analysed mitochondrial control region. Lizards from Montes do Pindo also showed some morphological differentiation, probably linked to the particular habitat where they occur, a relatively arid and rocky environment. We also present evidence of multiple paternity in some of the studied populations.

02-34 Poster

QUANTITATIVE AND NEUTRAL GENETIC VARIATION IN NORTHERN FRINGE POPULATIONS OF THE NATTERJACK TOAD

Björn E. Rogell [1]

[1] *Uppsala University/ ecology and evolution, population biology, Norbyv.18D, 75236, Uppsala, Sweden*

Bjorn.Rogell@ebc.uu.se

Populations on the margins of the distribution area of a species tend to be isolated and thereby harbor low genetic variation. The lack of genetic variation can pose a threat to the population's survival, but, on the other hand, the isolation can also facilitate local adaptation by limiting gene flow. In western Sweden the natterjack toad (*Bufo calamita*) lives on the margin of its distribution. Local extinctions, even of previously large populations, are known to occur in this area. We examined neutral genetic variation and population divergence using AFLP and quantitative genetics for larval history traits, which are known to be important fitness traits in amphibians. Full sib families' originating from six nearby islands (chosen on a priori assumptions about genetic variation in the populations) were reared in three temperatures (20°C, 27°C and outdoor). We found a well defined population structure with a global F_{ST} of 0.13, but no isolation by distance. The Q_{ST} was overall lower or roughly equal to F_{ST} indicating that there were no divergent responses to selection among the populations. We found a positive correlation between survival at 20°C and genetic variability among the populations, suggesting inbreeding depression. There were also correlations between life history traits and genetic variation. We found no support for local adaptation in the natterjack toad populations in the Swedish west coast. Extremely small Q_{ST} values in some of traits may suggest uniform selection among the localities. The correlations between life history traits and genetic variability also indicate that parts of the divergence might be mediated by effects of inbreeding depression. Additionally, we found correlations between genetic variability and environmental variance for life history traits, suggests that heritabilities might be affected by the inbreeding level.

02-35 Poster

INBREEDING AND GENETIC VARIABILITY IN A CAPTIVE BREEDING PROGRAMME OF ENDANGERED UNGULATES

María J. Ruiz-López [1], Eduardo R. S. Roldán [1], Gerardo Espeso [2], Montserrat Gomendio [1]

[1] *Museo Nacional de Ciencias Naturales (CSIC), Reproductive Ecology and Biology Group, 28028 Madrid, Spain*
[2] *Estación Experimental de Zonas Áridas (CSIC), Parque de Rescate de Fauna Sahariana, 04002 Almería, Spain*

mjruiz@mncn.csic.es

Captive breeding programmes are often established when endangered species have suffered a marked decline. Thus, founding populations tend to be small in size, and subsequent effective population size is generally constrained by space and funding limitations. This may result in loss of genetic diversity, which limits the ability of populations to adapt to environmental changes, and an increase in inbreeding, which decreases individual fitness. So far few studies have addressed the effects of the size of the founding population and subsequent management on levels of genetic diversity and inbreeding in captive breeding programmes. We studied three captive populations of endangered gazelles, *Gazella cuvieri*, *Gazella dorcas neglecta* and *Gazella dama mhorr*, kept at the Parque de Rescate de Fauna Sahariana (CSIC). For these three populations we combined pedigree data (inbreeding coefficients and founder analyses) with data derived from up to 26 microsatellite loci distributed across the genome, that were used to calculate genetic diversity. These three populations originated from a different number of founders, 4 for *Gazella cuvieri*, 11 for *Gazella dama mhorr*, and 22 for *Gazella dorcas neglecta*. As expected, levels of inbreeding were related to the size of the founding populations: lower in *Gazella dorcas neglecta*, intermediate in *Gazella dama mhorr* and higher in *Gazella cuvieri*. However, levels of genetic variability (heterozygosity, mean number of alleles) seem unrelated to the size of the founding population. We will discuss the reasons for the apparent discrepancy between levels of inbreeding and levels of genetic variability in these populations of endangered species.

02-36 Poster

LAKE OHRID ENDEMIC SALMONIDS: GENETIC AND MORPHOLOGICAL CHARACTERIZATION

Simona Susnik [1], Aleš Snoj [1], Steven Weiss [2]

[1] *Biotechnical faculty, dept. of Animal Science, Groblje 3, SI 1230, Domzale, Slovenia*
[2] *Karl-Franzens Universität Graz, Institut für Zoologie, Universitätsplatz 2, A 8010, Graz, Austria*

simona.susnik@bfro.uni-lj.si

Lake Ohrid endemics (*Salmo ohridanus* and Ohrid trout, putative *S. letnica*) were characterized by uni- (mtDNA sequences) and bi-parentally (microsatellite loci) inherited genetic markers analysis and 40 different morphological characters. Further exploring historical demography of both species, *Salmo ohridanus* was described as a highly divergent member of the genus *Salmo*. Based on comparative substitution rate differences in mtDNA and a rough age estimate of closely related *Salmo trutta* complex (i.e. at least 2 million years), the *S. ohridanus* probably split from a common ancestor of *S. trutta* >4 million years ago, which is consistent with minimum age estimate of the Lake Ohrid formation. Comparative analysis with Ohrid trout supports the notion that these fish have more recently colonized the lake and phylogenetically belong to the Adriatic lineage of *S. trutta*, which was estimated to expand 155,000 years ago. Nevertheless, based on microsatellite and mtDNA sequence variation the endemic Ohrid trout represents a monophyletic lineage, isolated from other Adriatic basin populations. In the interests of the unique biodiversity protection in this ancient ecosystem, we recommend retaining the taxonomic epithet *Salmo letnica* for the endemic Ohrid trout. Our results do not support the existence of population structuring within the lake, even though samples include two putative intra-lacustrine forms. Evidence of rare hybridization between *S. ohridanus* and Lake Ohrid brown trout exist at both mtDNA and microsatellite markers, but does not support the extensive introgression.

02-37 Poster

GENETIC STRUCTURE OF BLACK GROUSE POPULATIONS IN THE CZECH REPUBLIC

Jana Svobodová [1, 2], Jacob Höglund [3]

[1] *Czech University of Life Science, Department of Ecology and Environment, Faculty of Forestry & Environment, Kamýcká 1176, Prague 6 - Suchdol, CZ-16521, Prague, Czech Republic*
[2] *Academy of Sciences of the Czech Republic, v.i.i., Institute of Vertebrate Biology, Květná 170/8, CZ-603 65, Prague, Czech Republic*
[3] *Uppsala University, Population Biology, Department of Ecology and Evolution, Evolutionary Biology Centre, Norbyvägen 18D, SE-75236, Uppsala, Sweden*

svobodovajana@fle.czu.cz

Loss of suitable habitat and subsequent fragmentation of populations are recognized as important factors in species extinction, since genetic variability can be reduced in small populations and lead to the loss of evolutionary adaptability to environmental changes. In the Czech Republic (CR), numbers of Black Grouse (*Tetrao tetrix*) have been decreasing rapidly, especially during the second half of the last century. Nowadays the species occurs only in the borderline mountains where small populations are fragmented among islands of suitable habitat. This study examines genetic structure of CR black grouse populations using microsatellite nuclear markers amplified from feather samples. Although estimates of black grouse numbers are low, no populations have exhibited significant loss of heterozygosity. However, temporary increases of populations in polluted mountains and military areas during the 1980s may explain the high genetic diversity. We suggest to increase the connectivity of isolated populations by maintaining and creating corridors of suitable habitats for black grouse.

02-38 Poster

POPULATION STRUCTURE OF EUROPEAN GRAYLING, THYMALLUS THYMALLUS, IN FINLAND AND NEIGHBORING COUNTRIES

Akarapong Swatdipong [1], Mikko T. Koskinen [2], Jorma Piironen [3], Anti Vasemägi [1], Craig R. Primmer [1]

[1] *Turku university, department of Biology, Division of Genetics and Physiology, department of Biology, university of Turku, 20014, Turku, Finland*
[2] *Finnzymes Diagnostics, Finnzymes Diagnostics, Riihitontuntie 14 B, 02201, Espoo, Finland*
[3] *Joensuu Game and Fisheries Research, Joensuu Game and Fisheries Research, Kauppakattu 18-20, 80100, Joensuu, Finland*

akaswa@utu.fi

Due to the disturbance of natural habitats and exploitation for food, numerous indigenous fish species suffer fragmentation and reduction in population size. The European grayling, *Thymallus thymallus*, is one of most popular salmonid fish among recreational anglers in Finland and inevitably has been negatively affected by overfishing and non-indigenous fish introductions. In this study, 19 sampling sites throughout Finland and six populations from four neighboring countries were analyzed to evaluate the level of genetic variability and population structuring using 13 microsatellite markers. Consistent to the earlier studies even geographically closely related samples (<30 km) exhibited high levels of genetic differentiation indicating generally low levels of gene flow between populations. Nevertheless, a strong signal of isolation-by-distance was present both among Finnish populations and among all sampling sites. These preliminary results indicate that Finnish populations consisted of three main population groups corresponding to the northern, Baltic sea and south-eastern regions. A detailed conservation management plan for Finnish grayling will be presented.

02-39 Poster

THE SEARCH FOR GENETIC DISCONTINUITIES IN A RECENTLY EXPANDED SIKA DEER POPULATION IN JAPAN: TOWARD COARSE MANAGEMENT AND CONSERVATION OF LARGE MAMMALS

Haruki Tatsuta [1], Masanobu Yoshio [2], Tadashi Miyashita [2]

[1] *National Institute for Envirronmental Studies, Research Centre for Environmental Risk, 16-2, Onogawa, 3058506, Tsukuba, Japan*
[2] *The University of Tokyo, Graduate School of Agricultural Life Sciences, 1-1-1, Yayoi, 1138657, Tokyo, Japan*

htatsuta@nies.go.jp

Recent advances in landscape genetics allow us to obtain information on how landscape and environmental features influence population genetic structures. We adopted several landscape genetic tools for clarifying spatial patterns of genetic discontinuities in a recently expanded sika deer (*Cervus nippon*) population on the Boso Peninsula, central Japan. Our primary interest was to examine the effect of environmental features (e.g., mountain ridges, rivers, roads, dams) on the genetic structure of the sika deer population. After dividing the whole survey area into several meaningful blocks, we performed two independent spatial analyses (SAMOVA and network analysis based on Monmonier's algorithm) using mitochondrial D-loop and microsatellite data in order to search genetic discontinuities. We also implemented a Bayesian model that does not require *a priori* the determination of population units, using the microsatellite data. Although the level of genetic diversity was relatively low, we found distinctive spatial discontinuities that were consistent by the different searching algorithms. Based on these results, we will discuss historical process of population expansion of sika deer and explore units of population management and conservation.

02-40 Poster

THE EFFECT OF DISEASE ON NEUTRAL DIVERSITY OF FROGS.

Amber G. F. Teacher [1], Richard A. Nichols [2], Andrew A. Cunningham [3], Trenton Garner [3]

[1] *Institute of Zoology, Wildlife Epidemiology, Zoological Society of London, Regent's Park, NW5 1SU, London, UK*
[2] *Queen Mary, University of London, School of Biological and Chemical Sciences, Mile End Road, E1 4NS, London, UK*
[3] *Institute of Zoology, Wildlife Epidemiology, Zoological Society of London, Regent's Park, NW1 4RY, London, UK*

amber.teacher@ioz.ac.uk

Infections of ranavirus in UK populations of common frogs provide an example of an environmental change that affects populations severely. With this case study we can use empirical data to examine whether population genetic structure within and among populations is influenced by viral emergence.

We anticipate that the arrival of ranaviral infection will have imposed strong selection on parts of the genome, and that alleles conferring protection will have spread rapidly. It may be possible to detect this selection as a loss of genetic diversity at neutral loci linked to the newly advantageous alleles (due to genetic hitchhiking).

To give an indication of underlying neutral variation, a multiplexed 14-locus microsatellite system has been developed. Microsatellite genotyping has been performed for populations of frogs that are thought to have been infected with ranavirus for over 3 generations, and for populations that are thought have never been infected. This comparative method has shown that there is no overall significant difference in neutral variation (allelic diversity or heterozygosity) between disease-positive and negative sites within the UK.

02-41 Poster

LEVEL OF PHILOPATRY DETERMINES ASSIGNMENT OF LONG-LINE FISHING BYCATCH INDIVIDUALS IN THE VULNERABLE WHITE-CHINNED PETREL (PROCELLARIA AEQUINOCTIALIS)

Mareile N. M. S. Techow [1, 2], Peter G. Ryan [1], Colleen O'Ryan [2]

[1] University of Cape Town, DST/NRF Centre of Excellence at the Percy FitzPatrick Institute, Private Bag, Rondebosch, 7700, Cape Town, South Africa
[2] University of Cape Town, Molecular and Cell Biology, Private Bag, Rondebosch, 7700, Cape Town, South Africa

techow@science.uct.ac.za

The long-line fishing industry affects large numbers of seabirds, and mortality associated with this practice occurs on a global scale. Population specific information is lacking for most species, hindering assessment of magnitude and significance of seabird-fishery interactions. The White-chinned Petrel (WCP) breeds on remote islands within the Southern Ocean. Due to declining populations, it is considered vulnerable on the IUCN Red List; the species has the highest incidental mortality risk associated with the long-line fishing of all seabird species. In spite of this, no reliable estimates of historical populations exist and there are few monitoring studies in place. Colony level differences in dispersal and foraging areas in the WCP may cause variation in susceptibility to the fisheries by virtue of greater overlap between foraging and fishing areas. As a result a larger number of birds may be killed than is expected given their local colony size, thereby increasing the risk of local extinction. Limited tracking data suggests the species to be philopatric to natal colonies. The success of assignment depends on the presence of population structure, which is hypothesised given philopatry. Four methods were used to investigate the feasibility of using assignment tests to identify natal colonies; these included the use of mitochondrial cytochrome b sequence data, diagnostic single nucleotide polymorphisms in the cytochrome b gene, and two assignment algorithms that employ microsatellite data. Data for all markers suggested that foraging locations are largely separate for each ocean basin, with fisheries taking local birds. Results therefore suggest that WCPs are philopatric to ocean basins and the impact of a given fishery is likely confined to nearby colonies.

02-42 Poster

THE ROLE OF SUBSPECIES IN CONSERVATION. GENETIC ASSESSMENT OF MORPHOLOGICAL SUBSPECIES IN NW IBERIAN BUTTERFLIES OF THE GENUS EREBIA (NYMPHALIDAE: SATYRINAE)

Marta Vila [1], Nils Ryrholm [2], Mats Björklund [3]

[1] University of A Coruna, Department of Molecular and Cell Biology (Genetics), Faculty of Sciences, Campus da Zapateira, E-15008, A Coruna, Spain
[2] University of Gävle, Department of Mathematics, Natural and Computer Sciences, Kungsbäcksvägen 47, SE-80176, Gävle, Sweden
[3] Uppsala University, Department of Ecology and Evolution (Animal Ecology), Norbyvägen 18D, SE-75236, Uppsala, Sweden

mvila@udc.es

There is an ongoing discussion about the putative mismatch between named subspecies and genetically distinct populations, namely in birds. This controversy is severely affecting the writing process of the Lepidoptera volumes of the Iberian Fauna (http://www.fauna-iberica.mncn.csic.es/english/). This is because the subspecific nomenclature of Iberian butterflies is overwhelming. We aimed at revealing the genetic validity of some subspecies of *Erebia* butterflies, putatively endemic to NW Spain (e.g., *Erebia palarica castroviejoi*, *Erebia triaria mendesi*). For this, we sequenced mitochondrial genes (COI and AT-rich region) in several individuals from each intriguing subspecies and used haplotype networks to infer their degree of differentiation from other conspecific populations. This basic survey will be of great value in conservation terms. This is due to the fact that one of the criteria in which conservation managers of the regional administration are mostly interested in order to include a given taxon in the official Red List is the endemic status.

02-43 Poster

MOLECULAR DIVERSITY AFTER A RANGE EXPANSION IN HETEROGENEOUS ENVIRONMENTS

Daniel Wegmann [1], Mathias Currat [2], Laurent Excoffier [1]

[1] *University of Bern, Computational and Molecular Population Genetics Laboratory, Zoological Institute, Baltzerstrasse 6, 3012, Bern, Switzerland*
[2] *University of Geneva, Laboratoire d'Anthropologie, Génétique et Peuplements, 12 rue Gustave-Revilliod, 1227, Carouge, Switzerland*

daniel.wegmann@zoo.unibe.ch

Recent range expansions have probably occurred in many species, as they often happen after speciation events, after ice ages, or after the introduction of invasive species. While it has been shown that range expansions lead to patterns of molecular diversity distinct from those of a pure demographic expansion, the fact that many species do live in heterogeneous environments has not been taken into account. We develop here a model of range expansion with a spatial heterogeneity of the environment, which is modeled as a Gamma distribution of the carrying capacities of the demes. By allowing temporal variation of these carrying capacities, our model becomes a new metapopulation model linking ecological parameters to molecular diversity. We show by extensive simulations that environmental heterogeneity induces a loss of genetic diversity within demes and increases the degree of population differentiation. We find that metapopulations with low average densities are much more affected by environmental heterogeneity than metapopulations with high average densities, which are relatively insensitive to spatial and temporal variations of the environment. Spatial heterogeneity is shown to have a larger impact on genetic diversity than temporal heterogeneity. Overall, temporal heterogeneity and local extinctions are not found to leave any specific signature on molecular diversity that cannot be produced by spatial heterogeneity.

02-44 Poster

POPULATION SUB-STRUCTURE BETWEEN MALES AND WORKERS IN BOMBUS TERRESTRIS (HYMENOPTERA: APIDAE)

F.Bernhard Kraus [1], Stephan Wolf [2], Robin F. A. Moritz [2]

[1] *1El Colegio de la Frontera Sur (ECOSUR),,, Departamento Entomología Tropical, Línea de Investigación "Abejas de Chiapas", Carretera Antiguo Aeropuerto Km 2.5, C.P. 30700, Tapachula, Chiapas, México*
[2] *Martin-Luther-Universität Halle-Wittenberg, Biologie/Zoologie, Hoher Weg 4, 06099, Halle/S., Germany*

stephan.wolf@zoologie.uni-halle.de

Bumblebees (*Bombus*) are important pollinators in natural as well as in agricultural landscapes. However, only little is known abut their populations structuring and the mechanisms involved in geneflow between populations. In this study we analysed the population structure of two *B. terrestris* populations, one being situated in a Botanical Garden (Halle/Saale, Germany), and the other on a small Mediterranean island (Cabreara, Baleares, Spain) using microsatellite markers. We estimated the number of colonies contributing to the sampled workers and males, and assessed reproductive population sizes at both sampling locations. The colony number estimates for the island population, including both male and worker producing colonies, were significantly smaller (five colonies) then for the mainland population (32 and 42 colonies in two subsequent sampling years). The island population showed an overall heterozygosity excess, indicating a recent introgression event. In both populations all caught males originated from different colonies than the sampled workers, with a highly significant population subdivision between workers and males in case of the Botanical Garden population. The males originated from a much vaster area than the workers suggesting a spatial difference between the genetically effective population and the foraging population.

02-46 Poster

DEVELOPMENT OF A NON-LETHAL SAMPLING OF DNA FROM AN ENDANGERED MOTH FOR CONSERVATION GENETICS

Carlos Lopez Vaamonde [1], Marie-Anne Auger-Rozenberg [1], Neus Marí Mena [1], Francis Goussard [1]

[1] Institut National de la Recherche Agronomique (INRA) - Centre d'Orléans, Unité de Zoologie Forestière, 2163 Avenue de la Pomme de Pin, 45166, Olivet, France

carlos.lopez-vaamonde@orleans.inra.fr

Few studies have quantitatively assessed methods of non-lethal DNA sampling from insects for conservation studies. Here we develop a method of non-lethal sampling of DNA from adults of the threatened moth, *Graellsia isabelae* (Graëlls, 1849) (Lepidoptera: Saturniidae). This moth is protected by the Habitats Directive (the European Community initiative for an ecological network of special protected areas, known as "Natura 2000") and Bern Convention. Despite this protective legislation, there is no data at all on the population genetics of this moth.

Here we investigate methods for non-lethal sampling of DNA from *G. isabelae* adults and the effects of sampling on adult survivorship and mating behaviour. We test whether DNA sequence data can be reliably amplified from different tissues: i) a tarsal tip of a mid leg of an adult ii) a haemolymph sample and iii) a wing tip.

3

Behavioural EvoDevo

Tuesday August 21 *Location*: University building X

Symposium 3: Behavioural EvoDevo

ORGANIZERS: Rinaldo Bertossa, University of Groningen, The Netherlands
Leo Beukeboom, University of Groningen, The Netherlands

09.45-10.15	**Randolf Menzel** (invited) Small brains with smart minds
10.15-10.45	**Sebastian Haesler** (invited) An evolutionary perspective on FoxP2: from birds to humans
10.45-11.05	**Ryszard Maleszka** Genomic and epigenomic explanations of social behaviour in honey bees
11.05-11.35	*Coffee*
11.35-11.55	**Gro Amdam** Regulatory architectures of social design: dual function of TOR pathway in diphenic caste development and social behaviour
11.55-12.15	**Juergen Gadau** The evolution of sociality - Testing the reproductive ground plan hypothesis in ants
12.15-12.35	**Yannick Wurm** Genomic response to social restructuring of fire ant colonies
12.35-14.00	*Lunch*
14.00-14.20	**Guy Bloch** The molecular organization of the circadian clock and its socially mediated plasticity in the honey bee Apis mellifera
14.20-14.40	**Rinaldo Bertossa** Does fruitless specify male courtship behaviour in Nasonia vitripennis?
14.40-15.00	**Craig Walling** The quantitative genetic basis of parental care in the burying beetle (Nicrophorus vespilloides)
15.00-15.20	**Fredrik Sundström** From growth hormone to ecology: a transgenic coho salmon (Oncorhynchus kisutch) model
15.20-16.00	*Coffee*

03-01 Talk

SMALL BRAINS WITH SMART MINDS

Randolf Menzel [1]

[1] *Freie Universität Berlin, Biologie, Berlin, Germany*

menzel@zedat.fu-berlin.de

Animals are characterized at all levels of neural complexity by a continuous flow of energy, material and information. Behavior is an animal's means for surviving the destructive forces of entropy on both long and short time scales. Evolution maintains and in most cases improves complexity over multiple reproductive life cycles. Evolution in essence is an information-creating (in same cases -destructing) process, and the inherited information characterizing each organism may be called the species-specific phylogenetic memory. Animals also collect and store individual memories on a short time scale through learning by experience. Both kinds of memory, phylogenetic and individual memory, can be understood as organismic devices to predict the future and to reduce the environment's uncertainty. They are thus instantiations that link the past with the future, creating a present that is better adapted to the organism's requirements. Cognition can be viewed as the integrating process that utilizes both forms of memory, creates an internal representation of the world and a basis for expecting the future of the animal's own actions within the experienced environment. My presentation will deal with the question how cognition in animals with small brains may reach an impressive level of sophistication by integrating the two forms of memory. I shall focus on the honeybee and describe learning related tasks like navigation, communication, choice performance, application of rules, and expectation of outcomes. It is concluded that memories in these small brains are linked in such a way that across modality representations are created that allow the animal to make decisions on the basis of expected consequences of its own behavior. The question arises whether cognitive processes based on representations that allow internal evaluation of memories require a minimum brain size and particular neural organisation. It is concluded that brain size does not appear to be a limiting factor for cognitive processing of this kind. It is more difficult to evaluate neural processing as a limiting factor, and I shall present ideas that may be interpreted as design principles for cognitive processing.

03-02 Talk

AN EVOLUTIONARY PERSPECTIVE ON FOXP2: FROM BIRDS TO HUMANS

Sebastian Haesler [1]

[1] *MPI for Molecular Genetics/Freie Universität Berlin, Takustrasse 6, 14195, Berlin, Germany*

haesler@molgen.mpg.de

Language is a uniquely human trait, but few other species, among them whales, bats, and three orders of birds are capable of learning their vocal repertoire. The functional similarity between speech learning and song learning bears the question if this capacity for vocal learning involves similar molecular mechanisms. The first gene linked to human speech is the winged-helix/forkhead box transcription factor FoxP2, which was found to be mutated in individuals with severe difficulty articulating speech. Analysis of the molecular evolution of FoxP2 showed a high degree of conservation among vertebrates. Furthermore human *FOXP2* contains changes in amino acid (AA) coding and a pattern of nucleotide polymorphism that suggest it has been the target of selection during recent human evolution. We addressed the question of whether the FoxP2 gene has evolved differently in birds that learn their song from those whose song is innate by comparing the FoxP2 coding sequences from 8 avian vocal learners, 3 non-learners and a close non-avian relative, the crocodile. We did not find a relationship between the pattern of amino acid changes and the ability to learn songs. However, we cannot rule out that selection acted on the large regulatory sequence which were not analysed. Consistent with the sequence conservation, the FoxP2 expression pattern in the songbird brain is analogous to that of mammals, with strong expression in the basal ganglia, thalamus and cerebellum. Within the striatal song nucleus Area X, which is required for song learning, FoxP2 expression increases during times of song plasticity. To investigate whether there is a causal relationship between FoxP2 expression and song learning, we used lentivirus-mediated RNAi to reduce FoxP2 levels *in vivo*. Knockdown of FoxP2 results in impoverished song imitation, indicating that auditory-guided vocal learning in both humans and birds requires FoxP2. This suggests that the molecular substrate from which the uniquely human capacity of language evolved might not be exclusive to the hominid lineage.

03-03 Talk

GENOMIC AND EPIGENOMIC EXPLANATIONS OF SOCIAL BEHAVIOUR IN HONEY BEES

Ryszard Maleszka [1]

[1] *Australian National University, 0200, Canberra, Australia*

maleszka@rsbs.anu.edu.au

The genomic architecture underlying the evolution of insect social behavior is largely a mystery. With the honey bee genome assembly now available for scrutiny it appears likely that this highly social insect will be instrumental in addressing a number of important, but unresolved issues in the field of behavioural genomics that cannot be addressed appropriately in solitary animals. How a limited number of genes can generate virtually unlimited morphological and behavioral complexities? Are there unique genes for social behavior and if so, are they a special subset of the genome, or is the evolution of social behavior an example of the remarkable recruiting power of the nervous system?

Our analyses of the bee genome show that the transition from solitary life to integrated insect societies doesn't seem to correlate with obvious changes at the genomic level. One exception is the Royal Jelly Protein family that evolved from the ancient, multifunctional Yellow protein family and appears to be unique to *Apis*. Because individuals from the previous generation care for the young of the next generation, and determine their developmental fate (fertile queen versus sterile worker), all major aspects of eusociality in the bee are influenced by Royal Jelly. Like the insect Yellows, RJPs are multifunctional proteins with diverse, context-dependent physiological and developmental roles. Because RJ genes have thus far only been found in *Apis*, we speculate that they may have specifically evolved to modulate eusociality via nutrition. This suggests that alternative developmental trajectories of queens and workers must be controlled by an epigenetic mechanism that links the environmental signals (diet) with the genome.

The discovery of a family of conserved DNA methylases in *Apis* suggests that this species has the mechanism for storing epigenetic information that controls heritable states of gene expression. We will report on our ongoing efforts to silence the methylation system in the larva and on the effects of environmental changes on methylation, gene expression and queen development.

03-04 Talk

REGULATORY ARCHITECTURES OF SOCIAL DESIGN: DUAL FUNCTION OF TOR PATHWAY IN DIPHENIC CASTE DEVELOPMENT AND SOCIAL BEHAVIOR

Avani Patel [1], M. Kim Fondrk [1], Osman Kaftanoglu [1], Christine Emore [2], Greg Hunt [2], Gro V. Amdam [1]

[1] *Arizona State University*
[2] *Purdue University*

Gro.Amdam@asu.edu

Honey bees (*Apis mellifera*) provide a principal example of diphenic development. Excess feeding of female larvae results in queens (large reproductives). Moderate diet yields workers (small helpers). The signaling pathway that links provisioning to female developmental fate is not understood, yet we reasoned it includes TOR (target of rapamycin), a nutrient and energy sensing kinase that controls organismal growth. We examined the role of *Apis mellifera* TOR (amTOR) in caste determination by rapamycin/FK506 pharmacology and RNA interference (RNAi) gene knockdown. We show that in queen-destined honey bees, the TOR inhibitor rapamycin induces worker characters that are blocked by the antagonist FK506. Further, queen fate is associated with elevated activity of the *Apis mellifera* TOR encoding gene, *amTOR*, and *amTOR* gene knockdown blocks queen fate and results in individuals with worker morphology. A much-studied insect dimorphism, thereby, can be governed by the TOR pathway. In adult worker bees, RNAi further reveals that amTOR modulates the expression of the gene *vitellogenin*, which we recently established has multiple coordinating effects on social organization. Explicitly, *vitellogenin* gene activity paces the workers' age-associated transition from nest tasks to foraging in the field, and also affects foraging choice (i.e., collection of nectar vs. pollen) and lifespan. Associated molecular signaling pathways, therefore, appear to influence important aspects of both development and behavior in honey bees. Our results present the first evidence for a dual role of TOR in diphenic development and social behavior, and suggest that adoption of this ancestral nutrient sensing cascade can be an important basis for evolution of advanced sociality in insects.

03-05 Talk

THE EVOLUTION OF SOCIALITY - TESTING THE REPRODUCTIVE GROUND PLAN HYPOTHESIS IN ANTS

Juergen Gadau [1], Gro V. Amdam [1]

[1] *Arizona State University, SOLS, 85287, Tempe, USA*

jgadau@asu.edu

One major pattern in species evolution is the transition from solitary to social life histories. In order to understand how this transition can occur, it is important to know the regulatory mechanisms that underlie behavior, and how those mechanisms can be modified to create new behavioral phenotypes. One of the most extreme examples of divergence from a solitary life history is found in the eusocial insects (e.g. ants, termites, some bees), which exhibit a reproductive division of labor. Currently, there is limited understanding of the physiological and genetic control mechanisms that drive the division of labor, but recent findings in the eusocial honey bee (*Apis mellifera*) suggest that the ancestral regulatory controls governing the reproductive cycle have been modified to generate the maternal behaviors exhibited by the non-reproductive worker caste. Heterochronous shifts in expression of these traits may have enabled the decoupling of behaviors from reproductive events. This evolutionary framework has been termed the *reproductive ground plan* and it may be widely applicable for explaining the origins of the division of labor. We have tested some of the prediction from the reproductive ground plan in the harvester ant *Pogonomyrmex californicus* where queens forage during colony founding. Using workers and queens from *P. californicus* we determined if and how specific regulatory components of reproductive physiology (i.e., ovarian status and titers of juvenile hormone, ecdysteroids and vitellogenin expression) regulate *(i)* the sequential division of labor of a founding queen transitioning from an inactive virgin to a functional reproductive heading a colony, *(ii)* the division of labor between multiple founding queens that found a colony together, and *(iii)* the division of labor between workers.

03-06 Talk

GENOMIC RESPONSE TO SOCIAL RESTRUCTURING OF FIRE ANT COLONIES.

Yannick Wurm [1], John Wang [1], Laurent Keller [1]

[1] *University of Lausanne, Department of Ecology and Evolution, Biophore, 1015, Lausanne, Switzerland*

yannick.wurm@unil.ch

Division of labor between reproductive and non-reproductive individuals is a key characteristic of social insects societies. In ant colonies, both the number and reproductive status of queens can vary greatly over time. Little is known about the factors controlling which queens are reproductive, and nothing is known their genetic basis. Using gene expression microarrays, this study aims to identify what determines reproductive success among hundreds of candidate replacement queens in an orphaned fire ant colony.

A mature monogyne Solenopsis invicta fire ant colony includes a single queen, territory, thousands of workers and several hundred virgin queens. Upon the queen's death, many virgin queens shed their wings and begin reproductive development. They thus forgo a mating flight in hope of becoming the replacement queen. Over the following weeks, workers progressively execute almost all virgin queens that began reproductive development. The surviving virgin queen is thus "elected" to replace her mother.

The workers base their collective decision on cues provided by the virgin queens as reproductive development begins. In our artificial orphaning setup, two lineages of virgin queens compete in a colony of unrelated workers. We identified eight lineages of virgin queens that were more successful at becoming replacement queens in an orphaning situation, and eight lineages of queens that were less successful. Virgin queens were sampled from all 16 lineages before and after orphaning (20 minutes, 2, 6, and 24 hours post-orphaning). Their RNA was extracted, labeled and hybridized to cDNA microarrays, constituting a time-course of the expression for about 10,000 genes.

We describe the molecular-physiological changes occurring over time for the virgin queens of an orphaned colony, as well as the differences between lineages that may determine a queen's attractiveness to workers.

03-07 Talk

THE MOLECULAR ORGANIZATION OF THE CIRCADIAN CLOCK AND ITS SOCIALLY MEDIATED PLASTICITY IN THE HONEY BEE APIS MELLIFERA

Guy Bloch [1], Yair Shemesh [1], Hugh M. Robertson [2], Mira Cohen [1], Elad Rubin [1]

[1] The Hebrew University of Jerusalem, Evolution, Systematics, and Ecology, Jerusalem, Israel
[2] University of Illinois at Urbana-Champaign, Entomology, A. Silberman Institute of Life Sciences, 91904, Urbana, IL, USA

bloch@vms.huji.ac.il

The honey bee circadian clock is implicated in ecologically – relevant complex behaviors such as time sensing, and time compensated sun-compass navigation, and in social behaviors such as coordination of activity, dance language communication, and division of labor. We found that gene structure and function in the honey bee clock is more similar to the mouse than to Drosophila, and that socially modulated plasticity in circadian rhythms is mediated by plasticity in clock gene expression. The honey bee genome does not contain a true homolog to Drosophila *timeless (tim1),* has only the mammalian type *cryptochrome (cry-m*), and has a single orthologue for each of the other canonical "clock genes". In behaviorally rhythmic foragers, brain *amCry-m* oscillate with strong amplitude and a phase similar to *amPer* under both light-dark and constant darkness illumination regimes. By contrast to Drosophila, brain *amCyc* (*Bmal*) as in mice, oscillate with an almost anti-phase to *amPer*. Clock gene oscillations were strictly attenuated or totally suppressed in the brain of around-the-clock active nurse bees, even when synchronized by light. Phylogenetic analyses indicate that the basal animal lineage had both the mammalian and Drosophila types of *Cry* and *Tim*. Our results suggest that during evolution Drosophila specialized on using a set of clock gene orthologues that was lost by both mammals and bees, who in turn specialized on the other set. These findings raise critical questions concerning the evolution and the functional significance of species-specific variation in the molecular clockwork.

03-08 Talk

DOES FRUITLESS SPECIFY MALE COURTSHIP BEHAVIOUR IN NASONIA VITRIPENNIS?

Rinaldo C. Bertossa [1], L. Van de Zande [1], L. W. Beukeboom [1]

[1] University of Groningen, Evolutionary Genetics, Haren, The Netherlands

r.c.bertossa@rug.nl

Evo-Devo is shedding light on the interplay between evolution of forms and underlying developmental processes. Behaviour – a step forward in phenotypic complexity compared to morphology – has received less attention from the Evo-Devo field. One of the genes that could help to understand the relationship between development and evolution of complex behaviours is *fruitless*. Expression of male-specific *fruitless* transcripts in *Drosophila* is enough to specify male courtship behaviour in both adult males and females. *fruitless* belongs to the sex-determinig genetic cascade in insects of which different genes are conserved throughout metazoans. Males of the parasitic wasp *Nasonia vitripennis* court females with an elaborated courtship behaviour. We are analysing *fruitless* in *Nasonia* to understand whether it is playing a role in male courtship behaviour. Ongoing results will be presented.

03-09 Talk

THE QUANTITATIVE GENETIC BASIS OF PARENTAL CARE IN THE BURYING BEETLE (NICROPHORUS VESPILLOIDES)

Craig A. Walling [1], Clare E. Stamper [1], Per T. Smiseth [2], Allen J. Moore [1]

[1] University of Exeter, Cornwall Campus, Centre for Ecology and Conservation, Tremough, TR10 8EZ, Penryn, UK
[2] University of Manchester, School of Biological Sciences, M13 9PT, Manchester, UK

c.a.walling@exeter.ac.uk

Evolutionary resolutions for conflicts of interest over parental allocation of resources to offspring require a genetic basis to both parental provisioning and offspring solicitation behaviours. Despite this, empirical work has focused on phenotypic expressions of behaviour only, with experimental demonstrations of genetic variation in either parental provisioning or offspring solicitation extremely rare. We have studied the developmental and fitness consequences of parental care and family conflicts in a burying beetle, *Nicrophorus vespilloides* and now turn to an investigation of the genetic basis of parenting. We conducted a quantitative genetic experiment based on a half-sib breeding design and determined genetic and environmental contributions to variation in parental provisioning. Burying beetles (Nicrophorus spp.) breed on carcasses of small vertebrates and care can be expressed by either or both sexes and under uni- and bi-parental conditions. Offspring care involves multiple behaviours including direct provisioning of pre-digested carrion to the larvae, the removal of bacterial and fungal growth from the carcass and defence of the brood against predators. We examined several hundred full- and half-sib males and females caring for offspring under uni-parental male, uni-parental female and bi-parental conditions. We use these data to address, for the first time, the quantitative genetic basis to parental provisioning behaviours and also the genetic co-variation in behaviours between the sexes and between uni- and bi-parental conditions.

03-10 Talk

FROM GROWTH HORMONE TO ECOLOGY: A TRANSGENIC COHO SALMON (ONCORHYNCHUS KISUTCH) MODEL

Fredrik Sundström [1], Mare Lõhmus [1], Robert Devlin [1]

[1] Fisheries and Oceans and University of British Columbia, Centre for Aquaculture and Environmental Research, 4160 Marine Drive, V7V 1N6, West Vancouver, Canada

fredrik.sundstrom@zool.gu.se

We have studied how an experimentally increased intrinsic growth rate (through growth hormone transgenesis) has affected physiology, morphology and behavior in coho salmon on individual and population levels under various environmental conditions. The inserted transgene causes unregulated production of growth hormone which in turn causes faster embryonic development and an approximately 2-3 fold increase in scope for daily growth rate. Direct effects on phenotype by altered hormone production as well as indirect effect due to rapid growth have been observed. The magnitude of phenotypic effects varies with environment, with apparent gene-environment interaction determining phenotypic differences when compared to wild-type. Experiments in ecological settings suggest that a natural mutation with phenotypic effect similar to that of the transgene could persist and spread under certain conditions. Our work show how increases of a gene-product such as growth hormone can have pleiotropic effects with dramatic consequences for the biology of the animal, with many of the effect being very difficult to predict due to interaction with environmental conditions.

03-01 Poster

THE EFFECTS OF FOOD STRESS AT NYMPH AND ADULT STAGES ON REPRODUCTIVE DEVELOPMENT AND LIFE HISTORY TRAITS IN THE OVOVIVIPAROUS COCKROACH NAUPHOETA CINEREA

Emma L. B. Barrett [1], John Hunt [1], Allen J. Moore [1], Patricia J. Moore [1]

[1] *University of Exeter, Centre for Ecology and Conservation, Tremough Campus, TR10 9EZ, Penryn, UK*

elbb201@ex.ac.uk

One hypothetical mechanism for the trade-off between gametes and soma in female insects is oosorption, the resorption of mature unfertilised oocytes. While previous work focused on adult diet, juvenile environment may be more integral to life history decisions. We examined the effect of dietary stress during nymphal development and adult sexual maturation on mating behaviour, body size, somatic nutrient storage, investment in reproduction structures, and levels of oosorption through apoptosis. Our results uncover complicated patterns of life history tradeoffs, indicating that females are making decisions regarding the allocation and recuperation of resources to and from germ versus soma based on both past and current resource conditions, and adjusting their behaviour accordingly.

03-02 Poster

CAROTENOID AVAILABILITY INFLUENCES EARLY REPRODUCTIVE DECISIONS AND THEREAFTER NESTLING PERFORMANCE.

Anne Berthouly [1], Fabrice Helfenstein [1], Filiz Karadas [2], Heinz Richner [1]

[1] *University of Bern, Zoological Institute, 6 Baltzerstrasse, Bern, Switzerland*
[2] *University of Yüzüncü Yil, Department of Animal Science, Turkey*

berthoulyanne@hotmail.com

In birds females can modify early investment in current reproduction both by varying clutch size and/or the composition of the eggs and by manipulating hatching synchrony. Such breeding decisions can favour specific nestlings depending on their sex, hatching order and other factors. Since carotenoids in the egg yolk protect biological molecules against free-radical damage and promote maturation of the immune system, but are limited in nature. We predict that their availability will drive important breeding decisions. In a supplemental feeding experiment in a wild great tit (*Parus major*) population, we tested whether carotenoid availability during egg laying influences egg size, hatching asynchrony, clutch and brood sex ratio, and the correlation of these traits with nestling performance. We fed half of the parents with carotenoid-enriched food (C+ group), and a control group with non-enriched food (C- group). We then cross-fostered the eggs between nests on the 3rd day of incubation in order to separate maternal effects from post-laying effects. We found (1) a higher proportion of male eggs early in the laying sequence in both groups but a higher hatching asynchrony in the C+ group than in the control group. We then observed (2) a mismatch for several additional traits if the genetic mother and the foster mother came from different treatment groups as opposed to coming from the same treatment group. These included a lower hatchability of the eggs, fewer males among the first hatched eggs, and poorer nestling condition. The results suggest first that carotenoid supplemented females manipulate hatching asynchrony to provide a competitive advantage to the males, and second that the early reproductive decisions are matched to the reproductive strategies at incubation and post-hatching parental care.

03-03 Poster

A NEW METHOD FOR STUDYING THE CAUSES OF ASSORTATIVE MATING AND SEXUAL ISOLATION: APPLICATION IN A CASE OF SYMPATRIC AND PARALLEL ECOLOGICAL DIVERGENCE

Paula Conde Padín [1], Emilio Rolán-Alvarez [1]

[1] *universidad de vigo, bioquímica, genética e inmunología, as lagoas marcosende, 36310, vigo, spain*

paulavig@uvigo.es

Assortative mating for a particular trait or between ecotypes, incipient or true species are fundamental parameters to understand the evolution of traits and species. They are usually estimated by qualitative (like *IPSI*) and quantitative (Pearson correlation coefficient) indexes obtained from the whole population. Such strategy do not allow to estimate the individual contributions to the assortative mating. We propose to use a new estimator, the *ri* coefficient, an additive decomposition of the Pearson correlation coefficient, to estimate the individual contributions to the sexual isolation and the assortative mating, respectively. As an example of application we work with two ecotypes of a marine snail (*Littorina saxatilis*), living at different micro-habitats and shore levels, have evolved in sympatry and in parallel across the Galician rocky shore. These ecotypes differ in many traits due to differential adaptation. They meet, mate assortatively and partially hybridize at the mid shore where the two micro-habitats overlap. The partial sexual isolation observed has been claimed as a side effect of the size differences between ecotypes linked to a size assortative mating observed in most populations of this species. So, we use a set of mating pairs from *L. saxatilis* to show how they can be employed to investigate the causes of sexual isolation and size assortative mating. This index was able to find that sexual isolation (and size assortative mating) was determined in this species basically by the specimen size, in support of a previous claim, exclusively due to the males (unexpected).

03-04 Poster

PHYLOGENY, REPRODUCTIVE ISOLATION AND BIOLOGY IN THREE SPECIES OF AFRICAN STEM BORERS

Anne-Emmanuelle Félix [1]

[1] *INRA/IRD, Versailles, France*

afelix@versailles.inra.fr

Three stem borers (Lepidoptera: Noctuidae) belonging to the genus *Busseola,* closely related from classical systematic, develop in Kenya. *Busseola fusca* is on maize and sorghum crops, which it heavily damages. *Busseola phaia* and *Busseola segeta* develop only on native wild plants in different areas: on *Pennisetum* in West Kenya and *Panicum* in East Kenya respectively. Purpose of the study was (1) to determine phylogenetic history of these species and (2) to determine if gene flow or interbreeding can occur between them. Molecular and behavioural studies were undertaken as well as pheromone identification. A phylogenetic tree based on mitochondrial sequences display 3 clades corresponding to the 3 distinct species belonging to *Busseola* genus. Pairwise distance was 3% between *B. phaia* and *B. segeta* that can be considered as a sub-species; a distance of 6% between *B. fusca* and the others indicates that *B. fusca* has to be considered as a different species. Identification of each sex pheromone mixture showed that the three species shared the same four components in similar ratios, but *B. phaia* and *B. segeta* sex pheromone contained one component more. Dial periodicity of female calling behaviour showed that *B. fusca* and *B. phaia* reproductive behaviour did not overlap whereas it did for *B. fusca* and *B. segeta*. Cross attraction studies in wind tunnel involving *B. fusca* and *B. segeta* or *B. phaia* showed that each species can attract the other. The 5th pheromone component did not act as a factor of reproductive isolation.

All the results demonstrated that the structure of the three species relies more on geographic isolation and host plant specialisation than on reproductive isolation. Interbreeding capacities and descent survival are the next question to be answered

03-05 Poster

GENERATION-DEPENDENT FEMALE CHOICE: BEHAVIOURAL POLYPHENISM IN A BIVOLTINE BUTTERFLY

Magne Friberg [1], Christer Wiklund [1]

[1] *Stockholm University, Department of Zoology, Department of Zoology, Stockholm University, 10691, Stockholm, Sweden*

magne.friberg@zoologi.su.se

Climatic and biotic circumstances vary as seasons shift, and different cohorts of multivoltine species are likely subjected to different selection regimes. The bivoltine butterfly *Leptidea reali* (Réal's wood white; Lepidoptera: Pieridae) appears during May and June in central Sweden and has a partial second generation in late July. We manipulated both generations to appear simultaneously, and performed laboratory mating experiments that showed the presence of a behavioural polyphenism in mating propensity, which is induced during the developmental stages. Females of the summer generation expressed higher mating propensities than spring generation females. Spring females showed an increase in mating propensity with increasing age, while summer females accepted most matings already when they were only one or two days old. It is likely that larval time constraints, a lower abundance of males and a lower risk of accepting a male of their univoltine sister species *L. sinapis* (wood white) have relaxed selection on mate discrimination among summer generation females. A major challenge for future research is to further investigate the developmental pathways causing the polyphenism, and the adaptive implications of cohort-dependent behaviours.

03-06 Poster

SYMMETRY AND FITNESS IN WORKERS OF THE HONEYBEE (APIS MELLIFERA L.)

H. Michael G. Lattorff [1], Robin F. A. Moritz [1]

[1] *Martin-Luther-Universität Halle-Wittenberg, Institut für Biologie, Molekulare Ökologie, Hoher Weg 4, 06099, Halle (Saale), Germany*

lattorff@zoologie.uni-halle.de

Symmetry is usually tightly linked with individual fitness and thought to be selected through sexual selection. Symmetrical organisms are preferentially chosen as partners. We here present a study on the honeybee (Apis mellifera) excluding sexual selection as a possible driver selecting for symmetry. Usually workers are sterile and only increase their own fitness indirectly via the offspring of their mother queen. However, whenever the queen is lost also workers are able to reproduce directly by parthenogenesis. Under these queenless conditions, some workers will activate their ovaries and start laying eggs whereas the majority of the workers remain sterile. The reproductive workers clearly gain in inclusive fitness compared to the sterile workers because they produce own offspring and hence enhance their direct fitness component in addition to the indirect fitness. This parthenogenetic system thus allows for analysing direct fitness effects without the interference of mate choice or sexual selection on fluctuating asymmetry.

Using artificial insemination, we produced test crosses resulting in genetically similar workers. We tested these workers for their egg laying potential and found a strong segregation pattern for ovary activation and hence direct fitness in honeybee workers. A subsequent analysis of the wing symmetry patterns of reproductive and non-reproductive workers indicated a strong co-segregation with fitness. Reproductive workers showed a significantly higher symmetry for 14 wing characters than non-reproductive workers.

The high association of fitness and symmetry suggests that developmental homeostasis, which is influencing the symmetry of adult insects, is fundamental for increasing individual fitness.

03-07 Poster

HATCHING ASYNCHRONY AND EVOLUTIONARY CAUSES OF GROWTH TRADE-OFFS WITHIN BLUE TIT CYANISTES CAERULEUS BROODS

Mark C. Mainwaring [1], Ian R. Hartley [1]

[1] *Lancaster University, Biological Sciences, LA1 4YQ, Lancaster, United Kingdom*

m.mainwaring@lancaster.ac.uk

Many species of altricial birds hatch their young asynchronously, thereby creating an age and size hierarchy within the brood. Sibling competition for parentally provided food is therefore asymmetrical, and later hatched offspring have previously been shown to employ different growth strategies compared to their older and competitively superior siblings in an attempt to mitigate their competitive disadvantage. However, what causes the later hatched 'runts' to employ different growth strategies remains unclear. Therefore this study describes the results of an experiment that manipulated the hatching order of blue tit *Cyanistes caeruleus* clutches in order to investigate which of the three maternal manipulations of phenotype; namely hatching pattern, egg volume or hormonal titre; causes later hatched runts to employ alternative growth strategies.

03-08 Poster

EFFECTS OF HABITAT COMPLEXITY ON BEHAVIOURAL DEVELOPMENT

Olav Moberg [1], Anne G. V. Salvanes [1], Victoria A. Braithwaite [2]

[1] *University of Bergen, Department of Biology*
[2] *University of Edinburgh, Institute of Evolutionary Biology*

olav.moberg@bio.uib.no

Animals that undergo a habitat shift face a number of challenges as they move between habitats; for example, they may encounter new predator species and may be vulnerable as they adapt to their new surroundings. To meet these changes, many species expresses plasticity in several traits, ranging from pure behavioural changes to pronounced morphological or physiological responses, or combinations of these.

However, as certain response-patterns may prove beneficial only in specific life-history situations, the organism need to have some mechanisms regulating the timing when these traits start developing to avoid unnecessary expenditure of time and energy at stages when other traits should be given priority. Thus, we can expect certain cues to function as triggers to initiate developmental responses when the current situation demands it. These cues may be environmental or internal as well as defined developmental stages.

Here, we present an experiment investigating the effects rearing environment have on cod shoaling behaviour. We found that cod reared in enriched environment differed in terms of shoaling responses from those reared in a plain, standard hatchery environment. The shoaling tendency of fish from enriched tanks depended on and varied between test environments, while fish from plain environments responded similarly across test conditions. This indicates that fish exposed to an enriched environment have a higher behavioural plasticity, and thus an enhanced ability to adjust behaviour when their surroundings change.

Based on the results in the presented work, we will discuss how the physical environment may function as the connecting bridge between an organisms evolutionary potential and the development of a proper behaviour.

03-09 Poster

HIGH VARIATION IN PUTATIVE PHEROMONE BINDING RECEPTORS GR68A AND GR32A IN DROSOPHILA VIRILIS GROUP AND ITS ROLE IN EVOLUTION OF MATE RECOGNITION IN SIBLING SPECIES.

Nikolai S. Mugue [1]

[1] *Institute of Developmental Biology, 26 Vavilov St., 119034, Moscow, Russia*

mugue@mail.ru

Gustatory receptor Gr68a has been shown to be male-specific and expressed in a few sensitive bristles of forelegs of *D. melanogaster* male. Expression of this receptor is thought to be important in first steps of mating –touching and assessment of female by conspecific male.

We have sequenced complete *Gr68a* gene and its alternative spliceform *Gr32a* in all 12 species of *D. virilis* group – *D. litoralis, D. ezoana*, *D. lacicola, D. borealis, D. montana, D. flavomontana, D. kanekoi, D. virilis, D. a. americana, D. a. texana, D. novomexicana, and D. lummei.* These two proteins are products of alternative splicing . Every species of the group posses unique type of *Gr32a* receptor, with majority of amino acid variation concentrated in the first and second extra cellular regions, corresponding with ligand-binding position. Variation in *Gr68a* protein concentrated in transmembrane domains and can be attributed to specificity to hydrophobic pheromone ligand. Both receptors show remarkable sign of strong positive selection (high Na/Ns ratio) and could play an important role in speciation process in this species flock formation.

03-10 Poster

DEVELOPING TRANSGENICS FOR THE FIRE ANT, SOLENOPSIS INVICTA

Mingkwan Nipitwattanaphon [1], John Wang [1], Laurent Keller [1]

[1] *University of Lausanne, Department of Ecology and Evolution, Biophore, UNIL-Sorge, CH-1015, Lausanne, Switzerland*

mingkwan.nipitwattanaphon@unil.ch

The development of transgenesis for ants would permit functional characterization of genes important for social behavior. To date, neither transgenics nor RNA interference (RNAi) has been reported for ants. RNAi has been developed for many insect species including two eusocial species, the honey bee and the termite. While this has been fruitful at the individual level, for social behaviors it may be necessary to induce RNAi for many or all members of a colony and this may not be practical or feasible. A transgenic colony would circumvent this problem, for example by expressing double stranded RNA for a gene in all individuals. In addition, transgenics would permit misexpression, overexpression and rescue experiments.

We are developing transgenic protocols for the fire ant, Solenopsis invicta. In the fire ant, colony transgenesis requires surmounting two obstacles. The first is controlled laboratory mating and the second is the creation of transgenic males or queens. Using modified instrument insemination techniques we have successfully produced colonies with up to 10 workers. We are currently replicating and improving this technique to obtain more workers. To make transgenic animals we are attempting to transfer the gene encoding the Green Fluorescent Protein (GFP) using a transposon based approach. Our efforts and results will be presented.

03-11 Poster

SCENT OVER-MARKING HYPOTHESIS: A RELIABLE ASSESSMENT FOR COMPETITIVE ABILITY BY POTENTIAL MALE

Thangavel Rajagopal [1], Govindaraju Archunan [1]

[1] *Bharathidasan University, Animal Science, Department of Animal Science, Bharathidasan university, 620 024, Tiruchirappalli, India*

deer_raj@yahoo.co.in

In many groups of mammals odoriferous substance that act as semiochemicals are produced by cutaneous and sebaceous glands. These glands are common in carnivores and rodents and in most ungulates groups. Functions attributed to this gland secretion include communication of information about sex, identity, female breeding condition, territorial demarcation. Very little information is available on this subject. In this study we analysed data on preorbital gland over-marking by male blackbucks in an captive condition. The present study revealed that the frequency of scent over-marking is too high in dominant male followed by predominant as compared to subordinate males. This would indicate that over-marking is a general response to any scent mark that an animal encounter. Interestingly, the subordinate male deposit their preorbital gland secretion in the tree stick or bark in the breeding lek, after immediately the dominant male is agonistic contact between subordinate and seemed to be a threat signal and than encounter marking or endorsing on the subordinate marked area. This indicates that the counter marking is a specialized form of olfactory communication by which the dominant male is able to locate the scent marks and deposits in area scent marked by particular conspecific. Further, the dominant male increased their scent over-marking rates during heat period. This observation suggests that over-marking by males may play a role in male-male competition among blackbuck herd. Moreover, the higher frequency of scent over-marking is used counter marking to assess the relative dominance of competitive animals.

We conclude that dominant scent over-marking can serve as a permanent threat signal and help to control the subordinate behaviours such as scent marking, scent production and patrolling activity, in order to maintain the hierarchy and the avoidance of physical combat and successful mate.

03-12 Poster

EFFECT OF PARENTAL BEHAVIOUR ON NESTS PREDATION RISK IN NORTHERN LAPWINGS VANELLUS VANELLUS

Miroslav Šálek [1], Jana Svobodová [1, 2], David Rešl [3]

[1] *Czech University of Life Science, Department of Ecology and Environment, Faculty of Forestry & Environment, Kamýcká 1176, Prague 6 - Suchdol, CZ-16521, Prague, Czech Republic*
[2] *Academy of Sciences of the Czech Republic, v.i.i., Institute of Vertebrate Biology, Květná 170/8, CZ-603 65, Brno, Czech Republic*
[3] *Agency fo Nature Conservation and Landscape Protection of the CR, Nuselská 39, Prague 4, CZ-140 00, Prague, Czech Republic*

salek@fle.czu.cz

Behaviour of bird parents nearby their nests has been hypothesised an important factor of nest predation risk. Testing of this phenomenon in various species and habitats provided for inconsistent results. This study evaluates effects of parental behaviour during incubation on nest predation risk in conspicuous precocial northern lapwings *Vanellus vanellus* in highly fragmented agricultural landscape with diversified predator guilds. We found that nest predation risk was influenced neither by change-over of the parents at the nest or their incubation effort. However, predation rate on experimental artificial nests placed close to active northern lapwing nests was higher than on nests 50 m far away. We conclude that that some predator species might be stimulated by a presence of the parents nearby their nests and that aggressive attacks of colonial breeders are the most efficient protection of northern lapwing nests against predators.

03-13 Poster

TWO FREQUENINS IN FRUIT-FLIES: AN UNUSUAL CASE OF NON-DIVERGENCE AT THE PROTEIN LEVEL

Alejandro Sánchez-Gracia [1], Jesus Romero-Pozuelo [1], Alberto Ferrús [1]

[1] *Instituto Cajal, CSIC, Neurobiologia del Desarrollo, Av. Doctor Arce 37, 28002, Madrid, Spain*

alejandro.sanchez@cajal.csic.es

Drosophila Frequenin (Frq), the homolog of the mammalian Neuronal Calcium Sensor-1 (NCS-1), was the first characterized member of the class A proteins belonging to the NCS family. This protein is a high affinity calcium-binding protein with ubiquitous expression in the nervous system. The over-expression of Frequenin enhances neurotransmitter release and facilitation, strongly suggesting a role in the regulation of the release per synapse, axonal growth and button formation. In D. melanogaster, this calcium sensor is encoded by two genes (frq1 and frq2) likely originated by a tandem gene duplication event. Thus, the two genes are located in tandem in the same genomic region and their products maintain a strong amino acid sequence identity (95% identity, 10 amino acid differences). Concerning their temporal and spatial expression patterns, both genes are very similar, but frq1 shows systematically higher levels of gene expression. Here, we have analyzed the amino acid and nucleotide sequence variation at the two Frequenins in twelve species of the Drosophila genus. Surprisingly, while synonymous mutations have been prevalent in the evolution of the coding region, we found no amino acid replacement across orthologous copies, demonstrating the presence of strong functional constraints following gene duplication. In addition, the analysis of Frq protein evolution using more distant species (e.g. yeast, fish, amphibian or mammalian species) reveals that the 10 amino acid differences fixed between Frq1 and Frq2 could be involved in their functional diversification. Interestingly, the reduction or abolishment of Frq activity does produce neither lethality nor sterility; we are investigating possible behavioral effects in individual fitness. Also, we have initiated the characterization of the *cis*-regulatory regions responsible of frq1 and frq2 expression pattern in order to obtain insights into the functional significance of the presence of two Frequenins and to understand the evolutionary mechanisms responsible of the preservation of the two duplicates in Drosophila.

03-14 Poster

INHERITANCE OF PARENTAL FIDELITY AND ITS EFFECTS ON OFFSPRING DEVELOPMENT

Clare E. Stamper [1], Craig A. Walling [1], Chloe Bird [1], Per T. Smiseth [2], Allen J. Moore [1]

[1] *University of Exeter, Cornwall campus, Centre for Ecology and Conservation, Penryn, TR10 8EZ, Cornwall, UK*
[2] *University of Manchester, School of Biological Sciences, M13 9PT, Manchester, UK*

c.e.stamper@exeter.ac.uk

There has been considerable research focusing on parental provisioning and offspring solicitation behaviours, however, much less is known about the causes and consequences of variation in parental fidelity, i.e. the amount of time offspring are cared for before being abandoned. Theory predicts that the decision to abandon should be determined by the probability of future mating opportunities, and the value of the current brood, which may vary between sexes. Abandonment could therefore be a plastic response to a given set of environmental variables. Alternatively, variation in parental fidelity or abandonment may be under genetic control and may represent low caring, low fidelity and high caring, high fidelity phenotypes. Here we present the result of a large half-sib breeding design using the burying beetle *Nicrophorous vespilloides* to investigate the variation in parental fidelity and the consequences for offspring fitness. *N. vespilloides* breed on vertebrate carrion and parents provide care (including direct provisioning of food and carcass maintenance) under uni-parental (male or female) and bi-parental conditions for anywhere between 0 and 120 hours. By allowing sons and daughters from half-sib families to rear offspring under uni-parental or bi-parental conditions and recording measures of offspring fitness, including dispersal mass and development times over sequential life-history stages, we have some of the first data on the genetic variation in parental fidelity, the genetic co-variation between males and females and between uni- and bi-parental conditions and the consequences of this variation for offspring fitness.

03-15 Poster

ADAPTIVE LEARNING AND THE GENETIC EVOLUTION OF BEHAVIOUR

Beata Sznajder [1], Martijn Egas [1], Maurice W. Sabelis [1]

[1] *University of Amsterdam, Population Biology, Kruislaan 320, 1098 SM, Amsterdam, Netherlands*

sznajder@science.uva.nl

Modifications due to learning constitute an important route in the development of animal behaviour. In particular, adaptive learning, i.e. the learning that allows an individual to develop behaviour that renders higher fitness, has been proposed to play an important role in the genetic evolution of behaviour. Classical hypotheses postulate that learning either speeds up or hampers genetic evolution, predictions known in the literature as the guiding effect (Baldwin effect) or hiding effect, respectively. However, these predictions are characterized by unilateral consideration of the genetically determined components of behaviour as evolving separately from the learning ability. In fact, many theoretical models treat learning ability as a property that is constant across a population and through time. In contrast, empirical evidence shows that learning is an evolving trait in itself. Therefore, the classical hypotheses are fundamentally flawed and may produce predictions inconsistent with the evolutionary process taking place in nature.

We re-examine the effect of learning on evolution by placing it within a model of evolutionary interplay between the learned and genetically determined trait components. Specifically, we utilize the theory of vector calculus to follow the joint evolution of adaptive learning as well as genetically determined trait values in populations evolving on complex fitness landscapes. This approach allows us to determine the direction of the fastest evolutionary change and values of the genetically determined trait component and learning ability towards which the population evolves. We discuss how this effect of adaptive learning on genetic evolution of behaviour depends on the mode of natural selection (as determined by the location of the population on fitness landscape) and give prediction as to how this process feeds back in to the evolution of learning itself.

03-16 Poster

PHENOTYPIC PLASTICITY OF ANTIPREDATORY RESPONSE: THE PERSISTENT EFFECT OF INCUBATION TEMPERATURE ON ADULT BEHAVIOUR IN GECKOS

Marián Trnik [1], Lukáš Kratochvíl [1]

[1] *Faculty of Science, Charles University, Department of Ecology, Viničná 7, 12844, Praha 2, Czech Republic*

trnik@email.cz, lukkrat@email.cz

Phenotypic plasticity of physiological, morphological or behavioural traits induced by thermal differences during incubation are well-documented in many ectothermic animals including reptiles. However, it is much less clear whether such incubational effects can persist to adulthood and effect long-term fitness. In this study, we examined the effect of incubation temperature on adult antipredatory behaviour in captive Mexican banded geckos (*Coleonyx elegans*, Eublepharidae). The experimental geckos were incubated at three constant temperatures (26, 28, 30 °C) and subsequently kept under common conditions till adulthood. Adult antipredatory behaviour was tested using standardized test with moving object as a simulated predator. We found consistent effect of incubation temperature on gecko behaviour: the animals incubated at 30 °C were generally less active and showed smaller frequency of several stereotypic antipredatory behaviours. Our results suggest that temperature during incubation can permanently organize behavioural phenotype, which could be of high ecological and evolutionary relevance.

03-17 Poster

THE EFFECT OF INCUBATION TEMPERATURE ON SEXUAL BEHAVIOR IN TWO CLOSELY RELATED GECKOS WITH CONTRAST SEX-DETERMINING SYSTEMS (GSD VS. TSD)

Hana Váchová [1], Lukáš Kratochvíl [1]

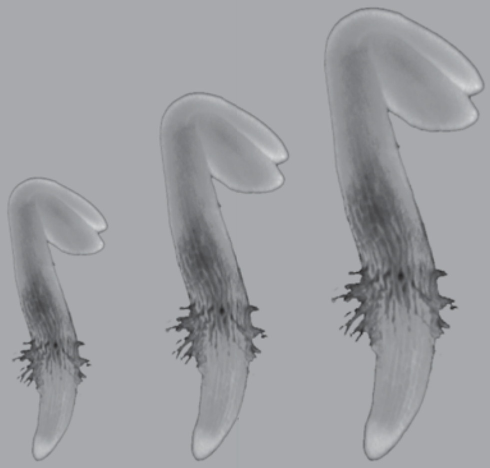
[1] *Charles University, Faculty of Science, Department of Ecology, Viničná 7, 128 44, Prague 2, Czech Republic*

hana.vachova@email.cz

In reptiles, the persistent influences of incubation temperature on the adult behavioral phenotype have been repeatedly documented. The behavioral phenotype established by the incubation temperature is deemed to be the selective agent responsible for the evolution and maintenance of temperature-dependent sex determination (TSD). Such temperature-established behavioral phenotypes have been demonstrated in the leopard gecko (*Eublepharis macularius*), the leading model reptile species in TSD research, where individuals of both sexes incubated at different constant temperatures strongly differ in sexual and aggressive behavior. It seems that males are most masculinized by temperatures producing maximum proportion of males in a progeny, while females from these temperatures are more or less behaviorally sterile. The closely related species *Coleonyx elegans* possesses genotypic sex determination (GSD), therefore equal sex ratios are produced at all incubation temperatures. Assuming the ancestral nature of TSD in this group, we predict that natural selection should lead to reduction of phenotypic plasticity in behavioral traits in GSD species. Otherwise, half of the individuals produced at given temperature would have suboptimal gender-specific phenotype.

Our recent contribution presents the first results of our research on the phylogenetic comparison of the influence of incubation temperature on behavioral phenotype within closely related gecko species differing in the mode of sex determination.

“Plant eco-devo”: ecology and genetics of life history timing in plants



Wednesday August 22 *Location*: University building IX

Symposium 4: “Plant eco-devo”: ecology and genetics of life history timing in plants

ORGANIZERS: Renate Wesselingh, Université Catholique de Louvain, Belgium
Henk van Dijk, Universite de Lille 1, France

09.45-10.15 **Sonia E. Sultan** (invited)
Eco-Devo variation in reproductive and offspring developmental timing
10.15-10.45 **Kathleen Donohue** (invited)
Completing the cycle: maternal effects as the missing link in plant life histories
10.45-11.05 **Juliette De Meaux**
Evolution of seed dormancy in Arabidopsis thaliana

11.05-11.35 *Coffee*

11.35-11.55 **Kristen Wagmann**
The variation in seed dormancy among Beta vulgaris subsp. maritima populations along a latitudinal gradient: impact of environmental factors
11.55-12.15 **Andrew M. Simons**
Variable selection on the timing of germination over multiple seasons and the evolution of diversification bet hedging
12.15-12.35 **Amy Strange**
Molecular basis of adaptive vernalization response

12.35-14.00 *Lunch, council*

14.00-14.30 **Outi Savolainen** (invited)
Genetics of adaptation: flowering time in Arabidopsis lyrata
14.30-14.50 **Benjamin K. Blackmann**
Connecting the sun to flowering in sunflower ecology and genetics
14.50-15.10 **Nora Scarcelli**
The effect of FRIGIDA on flowering time and its fitness value in an outbred population of Arabidopsis thaliana
15.10-15.30 **Renate A. Wesselingh**
Counting nodes: timing of flowering in the annual Rhinanthus angustifolius

15.30-16.00 *Coffee*

16.00-16.20 **Jutta Buschbom**
The impact of stand-specific timing of flowering on pollen-mediated gene flow across the landscape in Quercus petraea
16.20-16.40 **Antonina I. Internicola**
Should a food-deceptive species flower before or after a rewarding species? An experimental test of pollinator visitation behaviour under contrasting phenologies
16.40-17.00 **Jelmer A. Elzinga**
Synchronous flowering increases seed predation in small Silene latifolia patches:
a field experiment
17.00-17.20 **Elze Hesse**
Life history variation in contrasting habitats:
flowering decisions in the clonal perennial herb Veratrum album

04-01 Talk

ECO-DEVO VARIATION IN REPRODUCTIVE AND OFFSPRING DEVELOPMENTAL TIMING

Sonia E. Sultan [1]

[1] *Wesleyan University, Department of Biology, Middletown, CT, USA*

sesultan@wesleyan.edu

Eco-Devo life-history variation in plants includes adaptive and maladaptive plastic responses both within and across generations. These responses have been intensively studied in annual *Polygonum* species to understand the relation between ecological distribution and patterns of individual plasticity.

Parental plants subject to low light conditions may significantly delay reproductive onset and fruit production compared with plants receiving high light, a maladaptive response for annual species. Interestingly, this response varies among ecologically distinct taxa: species occurring in shaded habitats show less delay than congeners limited to open sites. This aspect of life-history timing can evolve rapidly, as is occurring in the exotic invasive *P. cespitosum*. Across generations, resource-deprived parental plants can alter the developmental timing of their offspring. These alterations vary among species, genotypes, and even architectural positions on the maternal plant. Drought-stressed parents in certain species produce drought-adapted seedlings with enhanced root extension rates; other species are unable to express this adaptive cross-generational plasticity for seedling developmental timing. Similarly, light-deprived parent plants produce seedlings with faster shoot growth and leaf production, a response which varies with the fruit's developmental position on the parent. Parental light as well as nutrient environment can also influence offspring germination rate, an eco-devo trait that varies among genotypes and therefore can evolve in response to local conditions.

04-02 Talk

COMPLETING THE CYCLE: MATERNAL EFFECTS AS THE MISSING LINK IN PLANT LIFE HISTORIES

Kathleen Donohue [1]

[1] *Harvard University, Organismic and Evolutionary Biology, 22 Divinity Ave., 02138, Cambridge, MA, USA*

kdonohue@oeb.harvard.edu

Through phenological plasticity, plants have the ability to affect the seasonal environment experienced by subsequent life stages. For example, germination timing determines the temperature and photoperiod experienced by young seedlings and later life stages, two cues that are important regulators of flowering time. The timing of flowering, in turn, determines the photoperiod and temperature during which seeds are matured and dispersed, seasonal factors that influence germination. The determination of the seasonal environment experienced by some life stages, and the plasticity of other life stages to those seasonal factors, govern the overall life history that a plant expresses. Field and laboratory experiments on Arabidopsis thaliana show how interactions between these two phenological traits can enable a bivoltine life history, and how natural selection on these traits—and on genes associated with variation in these traits—depends on the interactions between the timing of germination and flowering.

04-03 Talk

EVOLUTION OF SEED DORMANCY IN ARABIDOPSIS THALIANA

Juliette De Meaux [1], Marilyne Debieu [1], Sigi Effgen [1], Ilkka Kronholm [1], Maarten Koornneef [1]

[1] *MPI Plant Breeding Research, Genetics, Carl von Linne weg 10, 50829, Cologne, Germany*

demeaux@mpiz-koeln.mpg.de

Seed dormancy, is an important adaptive trait allowing plants to germinate at the optimal season of the year. We intend to understand the evolution of seed dormancy in the model plant species *Arabidopsis thaliana*. This species has recently undergone a range expansion which makes it a good model to study the evolution of life history traits related to the colonization of new climate spaces.

At the phenotypic level, the degree of seed dormancy follows a North-South gradient. In order to elucidate the genetic basis of this gradient, we examine nucleotide diversity at several genes involved in the control of seed dormancy. We conduct an analysis of the association between seed dormancy and diversity at genes known to influence germination timing and discuss genetic aspects of local adaptation for seed dormancy.

04-04 Talk

THE VARIATION IN SEED DORMANCY AMONG BETA VULGARIS SUBSP. MARITIMA POPULATIONS ALONG A LATITUDINAL GRADIENT: IMPACT OF ENVIRONMENTAL FACTORS

Kristen WAGMANN [1], Nina C. HAUTEKEETE [1], Yves PIQUOT [1], Henk VAN DIJK [1]

[1] *Universite Lille 1, Laboratoire GEPV UMR CNRS 8016, Bat SN2 Universite sciences et techniques de lille 1, 59655, Villeneuve d'Ascq cedex, France*

kristen.wagmann@ed.univ-lille1.fr

Dormancy prevents seed germination even in suitable environmental conditions. Theory suggests that dormancy (1) allows seedlings to grow in the right season for their survival and future reproduction, (2) allows populations to persist in unstable environments (through a seed bank) and (3) spreads germination in time so that there is less sibling competition. Sea beet (*Beta vulgaris* subsp. *maritima)* is supposed to have a partially genetically determined dormancy which could be broken by cold or drought. In the present study, we ask the following questions: what are the frequency and the distribution of seed dormancy in sea beet populations? How do climatic signals and dormancy affect germination timing? Is dormancy related to other factors like environmental disturbance or siblings' competition?

We sampled seeds from more than 100 French wild populations. Then we combined a greenhouse study with a field experiment in order to test: (1) how dormancy is distributed along a latitudinal gradient in France and among siblings ; (2) how this dormancy distribution is related to unstable environment ; (3) how climatic factors (rain and temperatures) affect dormancy releasing and germination phenology in the field.

Germination records show us, among other results, a high inter-population variability for dormancy with a significant latitudinal gradient from the Mediterranean populations (high dormancy) towards the Northern France populations (less dormancy). We also study the relationship between dormancy, sea beet life span, habitat stability and major climatic factors.

04-05 Talk

VARIABLE SELECTION ON THE TIMING OF GERMINATION OVER MULTIPLE SEASONS AND THE EVOLUTION OF DIVERSIFICATION BET HEDGING

Andrew M. Simons [1]

[1] *Carleton University, Department of Biology, 1125 Colonel By Drive, K1S 5B6, Ottawa, Canada*

asimons@ccs.carleton.ca

Fluctuating natural selection drives the evolution of bet-hedging traits; traits that appear to be suboptimal over short time scales but maximize longer-term fitness. The presence of phenotypic variance in traits such as seed germination and egg hatch timing is often interpreted as bet hedging, but there remains little support for this adaptive explanation. An adaptive explanation for diversification depends on knowledge of the degree to which natural selection on the trait fluctuates over time. Here I present results of a five-year manipulation study of fitness functions associated with variance in the timing of germination in Lobelia inflata (Campanulaceae). The complex fitness functions within years are found to show low similarity among years. Whether the observed level of environmental unpredictability can account for the evolution of the diversification trait in this species is discussed.

04-06 Talk

MOLECULAR BASIS OF ADAPTIVE VERNALIZATION RESPONSE

Amy Strange [1], Vincent Coustham [1], Clare Lister [1], Judith Irwin [1], Magnus Nordborg [2], Amity Wilczek [3], Johanna Schmitt [3], Caroline Dean [1]

[1] *John Innes Centre, Cell and Developmental Biology, Norwich, UK*
[2] *University of Southern California, Molecular & Computational Biology, Los Angeles, USA*
[3] *Brown University, Ecology and Evolutionary Biology, Rhode Island, USA*

amy.strange@bbsrc.ac.uk

Many plants need a prolonged period of cold, namely winter, before they are competent to flower. This is known as vernalization and during this process, *FLC*, the gene encoding a major *Arabidopsis* floral repressor is epigenetically silenced. We are using *Arabidopsis thaliana* accessions to elucidate the mechanism of *FLC* silencing, and to understand the molecular variation underlying the natural variation in vernalization response.

We have shown that *FLC* expression is similarly reduced in accessions during the first few weeks of cold, but the length of cold required to achieve stable epigenetic silencing of *FLC* is different. This variation appears to be correlated with adaptation to the length of winter. Using a QTL approach we are identifying the genes mediating variation in vernalization response. Common loci in six different populations account for the majority of this variation, with two loci mapping on top of *FLC* and *FRI*. FRI is a known up-regulator of *FLC*. We are investigating the hypothesis that variation in *cis*-elements in *FLC* is the major cause of adaptive variation in vernalization response. Defining the *cis*-elements, the corresponding *trans*-factors and the histone modifications affecting vernalization response will lead to better understanding of the molecular basis of *FLC* regulation. Combining this molecular analysis with population genetic studies and fitness measurements of plants grown in different climates is allowing us to understand the evolution of this adaptive trait, and is revealing the potential of a single gene to confer micro-climate adaptation on a global scale.

04-07 Talk

GENETICS OF ADAPTATION: FLOWERING TIME IN ARABIDOPSIS LYRATA

Outi Savolainen [1], Helmi Kuittinen [1], Anne Niittyvuopio [1]

[1] *University of Oulu, Department of Biology, 90014, Oulu, Finland*

outi.savolainen@oulu.fi

Adaptation to local conditions requires that timing of growth and reproduction of plants is synchronized with favorable conditions. Selection for adaptation has led to genetic differentiation in variation in flowering time and timing of growth. The genetics underlying these adaptations can now be studied with methods of population genomics.

Arabidopsis lyrata is a perennial outcrossing relative of *A. thaliana*. It is rapidly becoming an important model organism in ecological genetics. *A. lyrata* populations are known to show local adaptation in reciprocal transplant experiments and they are differentiated with respect to flowering time. We have examined the genetics of these differences by studying the role of different candidate genes in governing this variation. Flowering time has been characterized in multiple populations and environments. We have also examined sequence variation of genes of the *Arabidopsis thaliana* flowering pathways in the populations. Some genes have important roles in both in the selfing *A. thaliana* and the outcrossing *A. lyrata*, but the population genetic patterns of variation are different

04-08 Talk

CONNECTING THE SUN TO FLOWERING IN SUNFLOWER ECOLOGY AND GENETICS

Benjamin K. Blackman [1], Scott D. Michaels [1], Loren H. Rieseberg [1, 2]

[1] *Department of Biology, Indiana University, Bloomington, IN, USA*
[2] *Department of Botany, University of British Columbia, Vancouver, BC, Canada*

bkblackm@indiana.edu

Natural populations of the common sunflower, Helianthus annuus, display remarkable variation in flowering time and photoperiod sensitivity in flowering time. This variation is distributed along a latitudinal cline, with flowering occurring later and photoperiod sensitivity changing from day neutral to facultative short day to facultative long day as one moves from high to low latitude. A clinal pattern and Fst:Qst analysis indicate the geographic distribution of variation has been shaped by natural selection. To pinpoint the genetic variation underlying differences in photoperiod sensitivity, we have isolated and assayed expression of key candidate genes in plants from multiple natural populations raised in several photoperiods. Gene expression analysis indicates that the critical molecular differences that determine differences in plasticity to photoperiod lie in the very limited portion of the photoperiod pathway downstream of CONSTANS but upstream or in cis- to FT. Gradients in FT and SOC1 expression are also well associated with the clinal distribution of time to flower. Together, our data suggest that natural selection on transcriptional regulation of a single gene or gene family explains a great deal of the diversity of photoperiod sensitvity in flowering time observed in natural sunflower populations.

04-09 Talk

THE EFFECT OF FRIGIDA ON FLOWERING TIME AND ITS FITNESS VALUE IN AN OUTBRED POPULATION OF ARABIDOPSIS THALIANA

Nora Scarcelli [1], Paula Kover [1]

[1] *University of Manchester, Faculty of Life Sceince, Oxford Road, M13 9PL, Manchester, UK*

nora.scarcelli@manchester.ac.uk

Despite much interest, we still know very little about the molecular basis of adaptation. To improve our understanding it is necessary to combine knowledge of the genetic basis of traits under selection with information about how natural selection acts on the genetic variation available.

The model organism *Arabidopsis thaliana* is ideal to study the molecular basis of adaptation, because much is known about the genetic basis of flowering time, a key character for plant adaptation. The gene *FRIGIDA* (*FRI)* has been shown to explain a large proportion of the variability in flowering time among natural accession of *A. thaliana*. At this locus, the ancestral functional allele delays flowering unless vernalization occurs. Non-functional mutant alleles confer early flowering independent of vernalization, and are thought to have been selected during *Arabidopsis* range expansion after the last glacial period. Previous studies have investigated the effect of *FRI* in flowering time in natural accessions and mutant lines. However, linkage disequilibrium in these lines prevents estimation of the effect of *FRI* independent of other co-adapted genes. To investigate the effect of *FRI* on flowering time independent of the genetic background, we developed an outbred population by inter-mating 19 accessions.

Here, we present the effect of *FRI* in different life-history traits (bolting time, plant architecture and fitness) under two different growth conditions (simulating a summer-annual cycle and a winter-annual cycle). We show that the effect of *FRI* is environmentally dependent and that this locus probably has pleiotropic effects on other life-history traits. The relevance of this finding to the evolution of flowering time in *Arabidopsis* will be discussed.

04-10 Talk

COUNTING NODES: TIMING OF FLOWERING IN THE ANNUAL RHINANTHUS ANGUSTIFOLIUS

Renate A. Wesselingh [1]

[1] *Université catholique de Louvain, Unité d'Ecologie et de Biogéographie, Croix du Sud 4-5, B-1348, Louvain-la-Neuve, Belgium*

wesselingh@ecol.ucl.ac.be

The genus *Rhinanthus* (Orobanchaceae) consists of annual, bumblebee-pollinated hemiparasitic herbs growing in grasslands. It is known for its extensive variation in flowering time. Within many of the species, several ecotypic variants are distinguished. Vernal ecotypes flower early, have few branches and are relatively small. Aestival plants are bigger, have more branches and flower in mid-season, while autumnals have many branches and flower late. It has been recognised that these differences, which persist in common gardens, are linked to the number of nodes produced before the first flower, vernal plants producing few nodes and autumnals many.

My research is aimed at determining what underlies variation in flowering time within a vernal population of *Rhinanthus angustifolius*. Can within-population differences in flowering time explained by differences in node number, just as among ecotypes, or does variation in the timing of germination or differential growth rates contribute as well? Autumnal ecotypes have a much higher reproductive output than vernal plants. Does flowering time have an effect on plant fitness within a vernal population, are there differences in seed production between early and late flowering plants? What is the heritability of the number of nodes under the first flower?

These questions will be answered by observations on flowering time and fitness in a natural population, and experiments in greenhouse and garden.

04-11 Talk

THE IMPACT OF STAND-SPECIFIC TIMING OF FLOWERING ON POLLEN-MEDIATED GENE FLOW ACROSS THE LANDSCAPE IN QUERCUS PETRAEA

Jutta Buschbom [1], Bernd Degen [1]

[1] *Federal Research Center for Forestry and Forest Products, Institute for Forest Genetics, Sieker Landstr. 2, 22927, Grosshansdorf, Germany*

j.buschbom@holz.uni-hamburg.de

Pollen-mediated gene flow is one of the most important population-genetic processes in wind-pollinated tree species. Its extent determines not only the degree of outcrossing within forest stands, but also the cohesion of tree populations that are distributed across a landscape. A prerequisite of successful gene flow between forest stands in a region are overlapping windows of flowering times between tree populations of economic importance that might be of diverse origins. Integrating detailed observations of flowering periods with studies of gene flow patterns at local and regional scales, thus, forms the basis for forest breeding and management decisions and conservation strategies.

The extent of gene flow within and between different forest fragments was investigated using a parentage study and analyses of the differentiation of pollen pools in Quercus petraea growing in a highly fragmented landscape in northern Germany. Within the study area of radius 5 km the population of mature Q. petraea trees is predominantly distributed in three forest stands. The flowering phenology of randomly selected trees within the three forest fragments was recorded. All adult trees in the stands were genotyped. In addition, 20 offspring from each of 20 maternal trees within each of the three stands were genotyped. Unambiguous characterization of adult trees and progeny was ensured by genotyping all individuals at ten nuclear microsatellite loci. The results provide insight into the genetic disversity and spatial genetic structure within and between the stands and the impact of flowering patterns on the realized mating system, hybridization rates with co-occuring Q. robur and the patterns and rates of effective pollination events at different geographic scales.

04-12 Talk

SHOULD A FOOD-DECEPTIVE SPECIES FLOWER BEFORE OR AFTER A REWARDING SPECIES? AN EXPERIMENTAL TEST OF POLLINATOR VISITATION BEHAVIOUR UNDER CONTRASTING PHENOLOGIES

Antonina I. Internicola [1], Giorgina Bernasconi [1], Luc D. B. Gigord [1]

[1] *University of Lausanne, Department of Ecology and Evolution, Biophore University of Lausanne, 1015, Lausanne, Switzerland*

antonina.internicola@unil.ch

While many plant species offer rewards to pollinators in exchange for pollen transport, some species, particularly in orchids, lack rewards. Some characteristics of the deceptive species, which may interact with that of rewarding co-occurring species, may affect pollinator visitation rate by influencing how fast pollinators learn to avoid deceptive plants. We tested the effect of corolla colour similarity and relative temporal flowering order of rewarding and deceptive artificial inflorescences on visitation and learning by naïve bumblebees. We simulated partial overlap of the flowering phenologies of rewarding and deceptive plants. Deceptive plants received four times more visits when flowering alone after rewarding plants of similar colour than when flowering after dissimilar ones. This indicates that a deceptive species may benefit from flowering late in the season only if a similar rewarding species flowers before it. In addition, the visitation rate of deceptive plants that flowered before any rewarding species was independent of colour similarity. Also, when rewarding and deceptive plants were simultaneously available, pollinator learning was slower when the deceptive species flowered before the rewarding species than when flowering after the rewarding species. This suggests that early flowering may be a more widespread strategy for deceptive species to increase their reproductive success, irrespective of the similarity in floral cues between rewarding and deceptive flowers. This experiment suggests that there is considerable pressure on deceptive plant species to flower early in the season, which may have crucial implications for the evolutionary ecology and maintenance of deceptive species.

04-13 Talk

SYNCHRONOUS FLOWERING INCREASES SEED PREDATION IN SMALL SILENE LATIFOLIA PATCHES: A FIELD EXPERIMENT

Jelmer A. Elzinga [1, 2], Giorgina Bernasconi [2]

[1] *University of Jyväskylä, Departmnet of biological and Environmental Sciences, P.O. Box 35, 40014, Jyvaskylä, Finland*
[2] *University of Lausanne, Department of Ecology and Evolution, Biophore, 1015, Lausanne, Switzerland*

jelmeranne.elzinga@unil.ch

Pre-dispersal seed predation imposes strong fitness costs on plants, and is thus expected to contribute to selection on flowering phenology. Plants may evade pre-dispersal seed predation a) by flowering early or late in the season, or b) by flowering synchronously with conspecific neighbours to satiate the seed predators. Whereas the first strategy leads to prolonged flowering, the second strategy results in distinct flowering peaks. In addition, the number of neighbours, i.e. population size, may influence the optimal strategy and selection on phenological characteristics. We tested the seed predator–satiation hypothesis in different patch sizes in a field experiment with the white campion, *Silene latifolia* (Caryophyllaceae). It is naturally heavily attacked by the seed predating moth *Hadena bicruris* (Noctuidae). We created 24 patches (Synchronous vs. Asynchronous and Large vs. Small) by transplanting arrays of plants of different age classes. During thirteen weeks we measured realized synchrony, fruit predation, flower/fruit abortion and seed set per fruit. Plants experienced most fruit predation in synchronous small patches. In combination with higher abortion in small patches, plants in synchronous small patches produced fewer undamaged fruits. Within all patches, individual plants that flowered more synchronously with their neighbours, in general suffered increased fruit predation but aborted fewer flowers or fruits. Apparently synchronous flowering does not satiate the seed predators in this species, but instead it may increase patch attractiveness. However, no advantage of either synchronous or asynchrounous flowering was apparent in large patches, indicating that selection pressures on flowering phenology through biotic interactions strongly depend on patch, and thus population, size.

04-14 Talk

LIFE HISTORY VARIATION IN CONTRASTING HABITATS: FLOWERING DECISIONS IN THE CLONAL PERENNIAL HERB VERATRUM ALBUM

Elze Hesse [1, 2], Mark Rees [3], Heinz Müller-Schärer [2]

[1] *Oxford, Plant Sciences, South Parks Road, OX1 3RB, Oxford, United Kingdom*
[2] *Fribourg, Biology, Ecology & Evolution, Chemin du Musée, CH-1700, Fribourg, Switzerland*
[3] *Sheffield, Animal & Plant Sciences, Western Bank, S102TN, Sheffield, United Kingdom*

elze.hesse@plants.ox.ac.uk

Most species occur in a wide range of habitats and exhibit substantial demographic variation. Demographic heterogeneities between individuals can have considerable population dynamical consequences and can generate evolutionary change. Monocarpic plants are ideal systems for testing evolutionary ideas because the timing of flowering is a key determinant of fitness. The majority of monocarpic perennials have a relatively simple life history where reproduction is fatal and seeds are the only type of offspring produced. However, in many species although flowering is fatal for the ramet it is associated with the production of both seeds and vegetative offspring (e.g. *Veratrum album*). Here we investigate the selective pressures operating on the flowering strategy in *Veratrum album*. Data on ramet demography, collected over three years in fifteen populations, are used to parameterize several integral projection models. These are used to quantify the effects of habitat, seed predation and reproductive mode on the timing of flowering. Using the evolutionary stable strategy (ESS) approach, we predict the optimal flowering strategy – the relationship between flowering probability and size. Our results demonstrate that the ESS strategy differs among habitats, in excellent agreement with the observed flowering strategy. Furthermore, seed predation and reproductive mode have little effect on the ESS strategy. Using analytical approximations, we demonstrate that flowering decisions are predominantly determined by habitat-specific asymptotic sizes and are insensitive to changes in size-fecundity relationships. To conclude, habitat is an important aspect of the selective environment and is a significant factor in predicting ESS flowering strategies.

04-01 Poster

DIVERGENCE OF FLOWERING TIME AND FLOWERING TIME GENES BETWEEN ARABIDOPSIS LYRATA POPULATIONS

Esa A. Aalto [1], Anne Niittyvuopio [1], Päivi H. Leinonen [1], Helmi Kuittinen [1], David L. Remington [2], Outi Savolainen [1]

[1] *University of Oulu, Department of biology, P. O. Box 3000, FIN-90014, Oulu, Finland*
[2] *University of North Carolina at Greensboro, Department of Biology, P.O. Box 26170, NC 27402-6170, Greensboro, USA*

Esa.Aalto@oulu.fi

Timing of flowering is important to plant survival and reproduction. Differences in flowering characteristics among populations are likely due to adaptation to local environments, but may also evolve as a consequence of random divergence. Reciprocal transplant experiments have shown that *A. lyrata* populations are locally adapted and differ in important components of life history. Genes in the flowering time pathways of *A. thaliana* are likely to underlie the phenotypic variation in flowering traits. Thus, it is of interest to study the role of different evolutionary forces in shaping the variability at these loci, and to relate the nucleotide variation to patterns of phenotypic variation. We examine variation in flowering time in two common garden experiments in different conditions (Spiterstulen, Norway and Greensboro, North Carolina, USA). Further, we report on sequence variation in about 20 flowering time genes, studied in multiple populations. Polymorphism and divergence at individual flowering time loci are compared to general patterns.

04-02 Poster

THE PHYSIOLOGICAL BASIS OF THE GROWTH-SURVIVAL TRADE-OFF IN PLANTS: DO SLOW-GROWERS INVEST MORE IN STORAGE?

Rebecca Atkinson [1], Prof Mark Rees [2], Prof Mike Burrell [2], Dr Colin Osborne [2]

[1] *University of Sheffield, Animal and Plant Sciences, Western Bank, S10 2TN, Sheffield, England*
[2] *Animal and Plant Sciences, Western Bank, S10 2TN, Sheffield, England*

bop06rra@sheffield.ac.uk

The growth survival trade-off is recognised as being one of the major causes of variation in living things. The negative relationship between an individual's growth rate and its longevity is ubiquitous among taxa and results from a trade-off between investment in functional traits maximising one or the other. However, the mechanisms which underlie the growth-survival trade-off remain unclear.

Monocarps are semelparous plants and as a group are comprised of species which are polyphyletic in origin. These characteristics make the monocarps an ideal study group, especially as their life-history allows resource partitioning decisions to be relatively easy to discern.

We are investigating the physiological basis of the growth survival trade-off and are interested particularly in the costs associated with fast growth, for example when subject to environmental stress. The first step in this process is an analysis of the previously undescribed storage compounds of several monocarpic thistles, testing the hypothesis that slow-growth plants will invest more resources in root storage compared with fast growers. The differences in the types, amounts and relative proportions of the stored compounds allow species characterisation within the context of our research. The conclusions which can be made from this type of data are an essential part of understanding and comparing plant species' ecology.

04-03 Poster

ARF GENE FAMILY IN CARPEL EVOLUTION

Cédric Finet [1], Chloé Fourquin [1], Marion Vinauger-Douard [1], Annick Berne-Dedieu [1], Pierre Chambrier [1], Charlie P. Scutt [1]

[1] *Laboratoire de Reproduction et Développement des Plantes, Ecole Normale Supérieure de Lyon, 46, allée d'Italie, 69364, Lyon, France*

cedric.finet@ens-lyon.fr

The carpel, a novel type of female reproductive organ, arose specifically in an ancestor of the flowering plants, or angiosperms, and was probably a major factor in the evolutionary success of this group. We are investigating the molecular basis of carpel evolution by comparing the structure, expression and functions of carpel development genes in taxa whose lineages diverged at different stages in the evolution of the angiosperms. One such gene is ETTIN (ETT), which encodes a transcription factor of the auxin response factor (ARF) family in Arabidopsis thaliana. Interestingly, ETT (also known as ARF3) is truncated at its 3'-end by comparison to most other members of the ARF family, including its own close paralogue, ARF4. As a result, the ETT protein lacks two domains through which other ARF's are thought to interact with small regulatory proteins termed IAA proteins, resulting in the inactivation of ARF's as transcription factors. Despite their structural differences, ETT and ARF4 exhibit overlapping functions, as arf4 mutations increase ett mutant phenotypes in double mutant combinations.

We have analysed the molecular evolution of the ETT/ARF4 clade of the ARF gene family, starting from the earliest-diverging angiosperm lineages of the ANITA grade. Our results indicate the gene duplication event that separated the ETT and ARF4 lineages to have preceded the common ancestor of the extant angiosperms. However, we show that the truncation of the ETT gene occurred more recently, though before the divergence of the monocot lineage from that of the eudicots (including A. thaliana). We have also found evidence of parallel molecular evolutionary events involving 3'-truncations in the ARF4 orthologues of certain early-diverging angiosperm lineages.

04-04 Poster

CORRELATED VARIATION IN CIRCADIAN RHYTHM AND FLOWERING TIME AMONG NATURAL POPULATIONS OF CAPSELLA BURSA-PASTORIS (BRASSICACEAE)

Karl Holm [1], Ulf Lagercrantz [1]

[1] *Uppsala University, Department of Evolutionary Functional Genomics, Norbyvägen 18D, SE-752 36, Uppsala, Sweden*

karl.holm@ebc.uu.se

Circadian rhythms comprise a subset of biological rhythms with a period length of approximately 24 hours. The circadian clock(s) regulate many biological processes by synchronizing them with the environmental day/night cycles, that is, the photoperiod. Examples of processes regulated by the circadian clock include daily leaf movements, as well as the timing of crucial developmental transitions, such as the initiation of flowering. *Capsella bursa-pastoris* is a selfing tetraploid with disomic inheritance, which displays considerable genetic variation for flowering time, an important adaptive trait in plants. In an attempt to elucidate genetic factors influencing the variation in flowering time, the rhythmic expression of core components of the plant circadian clock, *TIMING OF CAB1* (*TOC1*) and *CIRCADIAN CLOCK ASSOCIATED1* (*CCA1*) have been measured in time series experiments conducted in constant light (LL), and under long day conditions (LD). Our results show that natural accessions of *C. bursa-pastoris* display considerable variation in circadian rhythm, which is correlated with phenotypic differences in flowering time. Further experiments will explore the causal genetic basis of this variation in circadian rhythm and its connection to variation in flowering time.

04-05 Poster

INTERACTIVE EFFECTS OF PAST SELECTION AND PRESENT CONSTRAINTS ON PLASTIC SHOOT ELONGATION

Heidrun Huber [1], Eric J. Von Wettberg [2], Niels P. R. Anten [3]

[1] *Radboud University Nijmegen, Ecology, Toernooiveld 1, 6525ED, Nijmegen, The Netherlands*
[2] *University of California, Davis, Ecology and Evolution, Ca 95616, Davis, USA*
[3] *Utrecht University, Plant Ecology and Biodiversity, Sorbonnelaan 16, 3584CA, Utrecht, The Netherlands*

H.Huber@science.ru.nl

In natural environments plants are subjected to different, often opposing selective forces. While shading induces the formation of taller and thinner shoots, mechanical stress tends to decrease shoot length and increase shoot diameter. Increased shoot elongation in response to shading will enhance light interception, but is also likely to increase the risk of physical failure. Conversely, the production of shorter and thicker shoots decreases the risk of physical failure, and at the same time, leads to a positioning of the leaves lower in the canopy. Early developmental decisions affecting shoot morphology and plant architecture can have long lasting effects on life-time fitness.

Change in shoot length can be achieved by plastic changes in two fundamentally different developmental processes: cell division and cell elongation. Our data show genetic variation in the relative contribution of cell elongation and cell division to shoot length and clear links of this to variation in biomechanical properties of plants. Plants originating from different habitats responded differently to shading and mechanical stimulation in terms of developmental growth rate, shoot length and biomechanical shoot traits. We found environment dependent costs and benefits associated to developmental, morphological and biomechanical shoot characteristics. We argue that understanding the interactive effects of past selective forces, timing of developmental processes and biomechanical consequences of plastic changes is important to understand ecological and evolutionary consequences of shade induced plasticity.

04-06 Poster

VERNALIZATION SENSITIVITY IN ARABIDOPSIS THALIANA: DIFFERENTIATION IN RESPONSE TO CLIMATIC FACTORS

Valérie Le Corre [1], Emilie Cadet [1]

[1] *INRA, UMR 1210 Weed Biology and Management, 21 000, Dijon, France*

lecorre@dijon.inra.fr

Vernalization sensitivity is a major factor determining flowering time in *Arabidopsis thaliana* ecotypes. Natural variation for vernalization sensitivity is largely controlled by the major flowering time gene *Frigida*. The recent observation of a latitudinal cline in vernalization sensitivity under short days (Stinchcombe *et al.*, 2005), and other pieces of evidence suggest that natural selection is acting on this trait. In order to confirm and extend this result, we have examined vernalization sensitivity in a set of *Arabidopsis* ecotypes originating from the natural species' range (mainly France, other European countries, and Russia). In a first experiment, flowering time was measured under natural, increasing day-length in a greenhouse after 0, 7, 14, 21 or 35 days of vernalization. In a second experiment, flowering time was measured under natural winter conditions in a common garden experiment located in Dijon, France. The genotype at *Frigida* was assessed for all ecotypes and association with vernalisation sensitivity was checked. Differences in vernalization sensitivity allowed the classification of ecotypes into several response groups. The ranking of ecotypes for flowering time was compared between the greenhouse and outdoor experiments. We present the results of statistical analyses testing for association between vernalization sensitivity and the following climatological data: monthly hours of sunshine, monthly precipitation, mean monthly number of rain days, mean monthly temperature, and mean monthly temperature range.

Stinchcombe JR *et al.* (2005) Vernalization sensitivity in *Arabidopsis thaliana* (*Brassicaceae*): the effects of latitude and FLC variation. Am. J. Bot. 92, 1701-1707.

04-07 Poster

THE EFFECT OF SEED BANKS ON POPULATION GENETIC STRUCTURE IN NATURAL POPULATIONS OF ARABIDOPSIS THALIANA

Sverre Lundemo [1], Hans K. Stenøien [1]

[1] *Norwegian University of Science and Technology, Biology, Realfagbygget, Høgskoleringen 5, 7491, Trondheim, Norway*

sverre.lundemo@bio.ntnu.no

High levels of genetic variability in natural populations of *A. thaliana* indicate that despite small census population sizes, the effects of genetic drift may be negligible at many sites. A reason for this could be the presence of seed banks that supplies the above-ground populations with genotypes preserved in the soil. In the presence of seed banks, the effective population sizes are expected to increase in local populations if individuals are recruited from gene pools spanning over several years and including occasional immigrants. Having a seed bank is also a form of insurance securing that some offspring will survive if environmental conditions are severe and/or fluctuating, thus buffering the plant population against environmental variability. Soil and seed samples from 26 Norwegian populations of *A. thaliana* have been grown in a green house, the resulting plants representing the below ground and the above ground cohort, respectively.

Genomic DNA from a total of 1060 individuals have been extracted and subjected to screening of SNP markers. The results of this analysis of below- and above-ground genetic structuring in *A thaliana* populations will be presented.

04-08 Poster

WOX GENE PHYLOGENY IN MONO- AND DICOTS: NEW ASPECTS OF EMBRYONIC PATTERNING

Judith Nardmann [1], Diego Durantini [1], Wolfgang Werr [1]

[1] *University of Cologne, Developmental Biology, Gyrhofstr. 17, 50931, Cologne, Germany*

j.nardmann@uni-koeln.de

In *Arabidopsis*, members of the *WUSCHEL homeobox* (*WOX*) gene family comprise earliest cell fate markers from the first zygotic divisions on (Haecker et al., 2004). Most members of the maize *WOX* gene family have been identified in the course of the phylogenetic identification of *WUS* orthologues from rice and maize (Nardmann and Werr, 2006). Their analysis has revealed major adaptations in *WUS* function in both grass species relative to the *Arabidopsis* model and more importantly, significant alterations and freedom for the specification of the shoot stem cell niche during angiosperm evolution. However, the *WOX* gene phylogeny also revealed that this gene family existed prior to the separation of mono- and dicot species. Based on pioneering work in *Arabidopsis,* members of the *WOX* gene family, therefore, were attractive candidates to be tested as molecular markers of embryonic pattering in maize. Here we describe the transcription patterns of *WOX* gene family members in the maize embryo. They uncover a significant degree of pattern conservation between maize and *Arabidopsis* embryos and reveal that the shoot/root axis in maize comprises a rather discrete domain from the proembryo stage on, which is distinct from that of the prospective scutellum.

04-09 Poster

MOLECULAR CHARACTERISATION OF SPODOPTERA FRUGIPERDA FROM THE CENTRE OF COLOMBIA

Clara Saldamando [1], A. M. Vélez [1], R. E. Arango [1], E. Aguilera [1]

[1] *Universidad Nacional de Colombia, Medellin, Colom bia, South America, Cll 65 cra 64, Medellin, Colombia*

cisaldam@unal.edu.co

Spodoptera frugiperda (J. E. Smith) is an agricultural pest whose larvae costly damages several crops including corn, rice, sorghum, some pasture grasses and cotton (Hazel *et al*. 2002, Lopez-Edwards *et al*. 1999). This pest has two "biotypes, one feeds on corn and sorghum, identified as "corn strain" and the other feeds on rice and bermudagrass and rice, identified as "rice strain" (Pashley 1986). These two biotypes are in their initial stages of speciation in the US (Pashley 1986) showing differential resistance to various insecticides and to *Bacillus thuringensis* (Adamczyck *et al.* 1997). Since these two biotypes are morphologically identical, molecular techniques have been used for thier identification in the laboratory (allozymes, AFLP´,s mithocondrial DNA and FR region) (Nagoshi y Meagher 2003, Pashley *et al*. 2004). However, no studies based on their genetics have been carried out in Colombia. The preliminary results obtained in this work have shown the presence of both biotypes at the centre of Colombia by using two molecular markers: COI region of the mitochondrial DNA which only amplifies on the corn biotype and the FR region, which is specific for the rice biotype.

04-10 Poster

ECOLOGICAL AND EVOLUTIONARY ASPECTS OF THE SEASONAL VARIATION IN MELAMPYRUM (OROBANCHACEAE)

Jakub Tesitel [1], Milan Stech [1]

[1] *University of South Bohemia, Faculty of Biological Sciences, Branisovska 31, Ceske Budejovice, Czech Republic*

jakub.tesitel@centrum.cz

Seasonal variation is a specific type of genetic variation determining architectural morphology of plants, which consequently affects their phenological features (timing of the onset of flowering and course of the seed production). A trade-off between early reproduction and total energy invested in the reproductive effort is supposed to induce this phenomenon widespread predominantly in annual hemiparasitic genera within the family Orobanchaceae.

We studied seasonal variation patterns in three species of the genus *Melampyrum*. Distinct seasonal ecotypes can be found in *Melampyrum nemorosum* displaying contrasting habitat preferences (hornbeam forests vs. meadows). Seasonal variation in *M. sylvaticum* and *M. pratense* has a rather continual character. Shifts in architectural morphological traits are mainly connected to the altitudinal gradient in the latter two species. Data from a fitness-oriented cultivation experiment on *M. sylvaticum* support the presence of the trade-off in the reproduction timing.

The early flowering populations are usually found in habitats where stress is the main limiting factor (mowing of meadows, short vegetative season on sites at timberline). The late ecotypes of the studied species grow mostly in communities where competition matters (forests in general). Hence we deduce that the seasonal variation is an important feature allowing shift on the S-C (stress-tolerance – competitiveness) continuum. Deviations from this general pattern can be explained by the history of the populations, e. g. descend of populations from timberline along man-made clearings and pathways, relict distribution of particular populations.

04-11 Poster

ARTIFICIAL SELECTION FOR FLOWERING DATE IN THE ITEROPAROUS PERENNIAL PLANT BETA VULGARIS SUBSP. MARITIMA (WILD BEET): AN ANALYSIS OF THE UNDERLYING MECHANISMS

Henk Van Dijk [1]

[1] *Université Lille 1, Laboratoire de Génétique et Evolution des Populations Végétales, bât SN2, 59655, Villeneuve d'Ascq, France*

henk.van-dijk@univ-lille1.fr

Flowering date in wild beet can easily be changed by artificial selection, a finding that is important in understanding the evolutionary potential with regard to climate change. At generation 13 in my long-term experiment (1 generation per year) plants were flowering about 40 days earlier under semi-natural conditions in the glasshouse (natural day length, temperatures slightly higher than outside, no frost).

The selection process was analysed by sowing all generations together in one big experiment in order to get an idea of the relative importance of the flowering induction pathways known in *Arabidopsis thaliana*: those associated with vernalization, photoperiod and gibberellins. After a variable cold period (0, 3, 6 or 9 weeks) and a subsequent exposure to increasing day lengths (3 min per day) at 16 ° C (to prevent devernalization) the day of the onset of flowering was recorded.

The results of this experiment are presented with special attention to the differences between the intensively studied semelparous species, in particular *A. thaliana*, and my own iteroparous study species

5

The population consequences of adaptive processes

Saturday August 25 *Location*: Ekonomikum 3

Symposium 5: The population consequences of adaptive processes

Organizers:	Daniel Rankin, University of Bern, Switzerland Jean-François Le Galliard, University Paris VI, France
9.45-10.15	**Nelson Hairston** (invited) The consequences of rapid evolution for community dynamics
10.15-10.45	**Maurice Sabelis** (invited) Milkers and Killers in a predator-prey metapopulation-feedbacks between ecological and evolutionary processes
10.45-11.05	**Ville-Petri Friman** Temporal fluctuations in prey resources drive the evolution of predator-prey interaction
11.05-11.35	*Coffee*
11.35-11.55	**Renee Duckworth** Evolution of behaviour at the edge of a range expansion
11.55-12.15	**Dylan Weese** Population recovery under selection on migrants: experimental evaluation in wild guppy populations
12.15-12.35	**Anssi Vainikka** Population-level consequences of evolution in size at maturation in herring-like fishes utilizing one or two resource niches
12.35-12.55	**Ilkka Hanski** Coupling of ecological and evolutionary dynamics in the dispersal of the Glanville fritillary butterfly
12.55-14.00	*Lunch*

05-01 Talk

THE CONSEQUENCES OF RAPID EVOLUTION FOR COMMUNITY DYNAMICS

Nelson G. Hairston, Jr. [1], Takehito Yoshida [1], Stephen P. Ellner [1], Laura E. Jones [1], Brendan J. M. Bohannan [2], Richard E. Lenski [3]

[1] *Cornell University, Ecology and Evolutionary Biology, Corson Hall, 14853, Ithaca, New York, USA*
[2] *University of Oregon, Biology, Eugene, Oregon, USA*
[3] *Michigan State University, Microbiology and Molecular Genetics, East Lansing, Michigan, USA*

ngh1@cornell.edu

Trophic relationships, such as between predator and prey or between pathogen and host, are a key interaction linking species in ecological food webs. The structure of these links and their strengths have major consequences for the dynamics and stability of food webs. The existence and strength of particular trophic links has often been assessed using observational data on changes in species abundance through time. My colleagues and I show that very strong links can be completely missed by these kinds of analysis when changes in population abundance are accompanied by contemporaneous rapid evolution in the prey or host species. Experimental observations, in rotifer-alga and phage-bacteria chemostats, show that the predator or pathogen can exhibit large-amplitude cycles while the abundance of the prey or host remains essentially constant. We know that the species are tightly linked in these experimental microcosms, but without this knowledge we would infer from observed patterns in abundance that the species are weakly or not at all linked. Mathematical modeling shows that this kind of cryptic dynamics occurs when there is rapid prey or host evolution for traits conferring defense against attack, and the cost of defense (in terms of tradeoffs with other fitness components) is low. Several predictions of the theory developed to explain the rotifer-alga experiments are confirmed in the phage-bacteria experiments where bacteria evolution could be tracked. Modeling suggests that rapid evolution may also confound experimental approaches to measuring interaction strength, but identifies certain experimental designs as being more robust against potential confounding by rapid evolution.

05-02 Talk

MILKERS AND KILLERS IN A PREDATOR-PREY METAPOPULATION-FEEDBACKS BETWEEN ECOLOGICAL AND EVOLUTIONARY PROCESSES

Maurice W. Sabelis [1]

[1] *University of Amsterdam, Section Population Biology, Institute of Biodiversity and Ecosystem Dynamics, Kruislaan 320, 1098 SM Amsterdam, The Netherlands*

sabelis@science.uva.nl

Both in the field and in the laboratory, specialist predatory mites tend to overexploit local populations of their prey, a herbivorous spider mite. While such predator-prey systems are shown to persist at a metapopulation scale, it remains puzzling why the predators do not disperse until after they have driven local prey populations to extinction (termed Killer strategy). In other words, why do predators not relax predation pressure (by earlier dispersal or killing less prey)? They might then profit later from the increased prey availability (termed Milker strategy). However, multiple invasions of predators in a local prey population will give rise to competition among Milkers and Killers and this tends to end in a victory for the Killers. While this seems an attractive explanation for the existence of Killers in the field, it hinges on the occurrence of multiple invasions and thereby on the ecological dynamics of the predator-prey system. Simulations of predator-prey metapopulation dynamics show that feedbacks between ecological and evolutionary processes promote Milkers, rather than Killers. This prediction has triggered thought on alternative explanations for the predominance of Killers in the field.

05-03 Talk

TEMPORAL FLUCTUATIONS IN PREY RESOURCES DRIVE THE EVOLUTION OF PREDATOR-PREY INTERACTION

Ville-Petri Friman [1], Jouni T. Laakso [1], Maija Orava [2]

[1] *University of Helsinki, Department of Environmental and Biological Sciences, P.O.X. 65, 00014, Helsinki, Finland*
[2] *University of Jyväskylä, Department of Environmental and Biological Sciences, P.O.X. 35, 40014, Jyväskylä, Finland*

ville.friman@helsinki.fi

Theory predicts that both predation and fluctuations in environmental conditions can drive the evolution and ecology of predator-prey interaction. However, little experimental data exists testing the combined effect of these factors. Here we report results of an evolution experiment where prey bacteria Serratia marcescens were exposed to predatory protozoa Tetrahymena thermophila in stable and temporally fluctuating food resource for approximately 1300 prey generations. The experimental system consisted of 30 aquatic microcosms and computer-controlled resource flow system. The factorial experiment included control treatments where both species lived alone (T. thermophila feeding on nonliving food). The resource flow was continuous in stable environment whereas in fluctuating environment it had 10-day wavelength. The average resource flow rate was equal across all treatments. The microcosms were sampled weekly for population sizes and to assess competition- and predation related traits in separate experiments. The fluctuating environment maintained higher population sizes of prey but only in the absence of the predator. Predators also had larger population sizes in the environment where prey resources fluctuated. As a result, predator to prey ratio was also highest in fluctuating environment. During the experiment this difference however decreased due to evolutionary increase in prey defense. Measurements of the prey antipredatory traits in different resource levels suggested that prey defense was energetically costly. The prey populations were equally defended in nutrient limiting conditions, but in the abundance of resources the prey that shared evolutionary history with predator outperformed the control prey. Interestingly, prey defense became stronger in the stable environment. Our results suggest that both predation and environmental variation are important factors affecting the ecological and evolutionary dynamics of predator-prey interaction.

05-04 Talk

EVOLUTION OF BEHAVIOR AT THE EDGE OF A RANGE EXPANSION

Renee A. Duckworth [1]

[1] *University of Edinburgh, Institute of Evolutionary Biology, West Mains Rd., EH10 5JX, Edinburgh, UK*

renee.duckworth@ed.ac.uk

Interspecific competition is an important evolutionary force that shapes the phenotypes and influences the geographic ranges of species. Yet, we know little about the evolutionary dynamics of competitive interactions, particularly at species borders. I combine quantitative genetic approaches with large scale field experiments to test the effects of individual variation in competitive behavior on population level processes that ultimately determine the distribution of species. Western bluebirds (*Sialia mexicana*) provide a unique opportunity to investigate the evolutionary consequences of competition because they are undergoing a rapid range expansion in which they are displacing mountain bluebirds (*S. currucoides*), a closely related congener. Using a long-term data set, I measured current selection and conducted heritability analysis on multi-generational pedigrees to show that, in western bluebirds, aggression evolves rapidly across the range expansion in response to spatial variation in the intensity of competition in edge versus interior populations. Evolutionary changes in aggression facilitate the range expansion because, on the one hand, decreased expression of aggression in interior populations where competition is relaxed minimizes its costs, yet at the same time, maintaining a highly aggressive invasion front enables western bluebirds to colonize new populations despite intense competition from mountain bluebirds. These results show that rapid evolutionary changes in behavior can have large-scale ecological consequences and ultimately affect the distribution of species over space and time.

05-05 Talk

POPULATION RECOVERY UNDER SELECTION ON MIGRANTS: EXPERIMENTAL EVALUATION IN WILD GUPPY POPULATIONS.

Dylan J. Weese [1], Michael T. Kinnison [1]

[1] *University of Maine, Biological Sciences, Murray Hall, 04469, Orono, Maine, United States*

dylan.weese@umit.maine.edu

The "rescue effect" predicts that immigrants may serve to sustain demes subjected to environmental perturbations and collapse. However, differential selection on migrants and residents can alter the expectations for local population recovery compared to a strictly ecological model. Populations of Trinidadian guppies are locally adapted to alternative predation regimes within coastal river systems where gene flow is biased from low-predation (upstream) into high-predation (downstream) demes. Recently, heavy flooding decimated the high-predation demes of the Marianne River, whereas low predation demes remained largely intact; presenting us with a serendipitous opportunity to experimentally evaluate the demographic consequences of selection on migrants during population rebound. We used mark-recapture and genotyping approaches to evaluate patterns of natural and sexual selection acting on migrant (low-predation) and resident (high-predation) guppies in a high-predation habitat, and quantify the relative demographic contributions of these ecotypes to subsequent recruitment and population growth. Our findings suggest very strong selection against immigrants that helps preserve mean population fitness but also likely slows the rate of population recovery relative to ecological expectations.

05-06 Talk

POPULATION-LEVEL CONSEQUENCES OF EVOLUTION IN SIZE AT MATURATION IN HERRING-LIKE FISHES UTILIZING ONE OR TWO RESOURCE NICHES

Anssi Vainikka [1], Anna Gårdmark [1], Åke Brännström [2], David Boukal [3], Ulf Dieckmann [4]

[1] *Swedish Board of Fisheries, Institute of Coastal Research, Box 109, 742 22, Öregrund, Sweden*
[2] *University of Umeå, Department of Mathematics and Mathematical Statistics, Umeå Universitet, 901 87, Umeå, Sweden*
[3] *Institute of Marine Research, P.O. Box 1870 Nordnes, 5817, Bergen, Norway*
[4] *International Institute of Applied System Analysis, Evolution and Ecology Program, Schlossplatz 1, A-2361, Laxenburg, Austria*

anssi.vainikka@fiskeriverket.se

Evolution towards smaller size at maturation, for example as a result of size-selective fishing, may not only hamper population productivity for harvest, but may also endanger recruitment. We studied population-level demographic consequences of evolution in maturation size using a physiologically size-structured seasonal model parameterised for Baltic herring (*Clupea harengus membras*). The effects of size-selective mortality and resource availability on the evolution of maturation size, and the evolutionary feedback from demography via density-dependent growth and size-dependent maternal effects were studied using adaptive dynamics techniques. We found that the existence of an ontogenetic niche shift at a size close to that of maturation reduced changes in maturation size in response to size-selective mortality and to changes in the availability of resources. This was because small individuals could outcompete larger fish as plankton feeders without the ontogenetic niche shift. The results are discussed in the light of fisheries-induced evolution and with regard to current fisheries management practices addressing ecosystem functioning.

05-07 Talk

COUPLING OF ECOLOGICAL AND EVOLUTIONARY DYNAMICS IN THE DISPERSAL OF THE GLANVILLE FRITILLARY BUTTERFLY

Ilkka Hanski [1]

[1] *University of Helsinki, Biological and Environmental Sciences, Viikinkaari 1, PO Box 65, 00014, Helsinki, Finland*

ilkka.hanski@helsinki.fi

Naturally segregating variation in the phosphoglucous isomerase (Pgi) locus in the Glanville fritillary butterfly (Melitaea cinxia) influences flight metabolic performance and dispersal rate. The Glanville fritillary occurs in multiple semi-independent habitat patch networks in the Åland Islands, Finland, with much variation among the networks in the number and spatial configuration of the constituent habitat patches. The frequency of the allele (Pgi-f) associated with high dispersal rate is highest in networks with the smallest number of patches and smallest average population size. This result implies that habitat loss and fragmentation selects for increased dispersal rate. The genetic composition of the metapopulation inhabiting a patch network affected the pattern of its temporal change. For a given change in the pooled size of the metapopulation, metapopulations with high frequency of Pgi-f showed high rate of establishment of new populations, whereas those in which the frequency of the alternative common allele Pgi-d was high showed low rate of colonization. These results demonstrate close coupling of ecological and evolutionary dynamics and how habitat fragmentation may impose a selection pressure on dispersal (and correlated life-history traits) in metapopulations.

05-01 Poster

REPRODUCTIVE STRATEGY OF VIRGIN FEMALES IN A PARASITOID WASP MELITTOBIA

Jun Abe [1], Tabitha M. Innocent [1], Sarah E. Reece [1], Stuart A. West [1]

[1] *University of Edinburgh, Institute of Evolotionary Biology, West Mains Road, EH9 3JT, Edinburgh, UK*

jun.abe@ed.ac.uk

Hymenopteran insects (e.g. wasps, ants, bees) have haplo-diploid sex determination, and so virgin females are able to produce (haploid) male eggs. In the genus *Melittobia*, virgin females lay only a couple of male eggs, and then wait with these offspring till their emergence, to mate with their own sons. Here we examine if virgin females adjust their egg laying behaviour if they lay eggs in the presence of another mated female. In this case we would expect the virgin female to lay a larger clutch of eggs, because her sons can mate with the daughters of the mated female. To test this hypothesis, we allowed a virgin and mated females to lay eggs on the same host. As a result of distinguishing their sons with a microsatellite DNA marker, the virgin females produced only slightly larger male clutches. However, in contrast to our prediction, the clutch size was much smaller than total clutch size of mated females. A possible explanation for this is that females are saving resources for future clutches after mating.

05-02 Poster

FROM THE IDEAL FREE DISTRIBUTION TO "OPTIMAL DISTRIBUTION": A SIMPLE GENERAL MODEL OF THE EVOLUTION OF DISPERSAL IN VARYING ENVIRONMENTS

Robin AGUILEE [1], Jean-Michel GUILLON [1]

[1] *Université Paris Sud, Laboratoire Ecologie, Systématique et Evolution (UMR 8079), Bâtiment 362, 91405, Orsay, France*

robin.aguilee@inapg.fr

Dispersal is a life history trait which has important consequences, in particular on the demography, dynamics, and genetic structure of natural populations. Many different dispersal strategies have been described. We developed a simple two-patch model of the evolution of dispersal in a spatially and temporally varying environment, for both animals and plants. Using game theory, we looked for evolutionary stable strategies when dispersal strategies depend on habitat and/or sex. We studied the influence of habitat selection, dispersal costs and primary sex-ratio. We determined conditions for the evolution of sex-biased dispersal. Our model can explain most of the results of previous different models including: when the environment varies in space and time, dispersal is favoured; when the environment varies in space only, dispersal is neither selected for nor against; sex-biased dispersal appears when the number of dispersal events is different between males and females. The simplicity of the model allowed us to demonstrate many results analytically. The strength of this model holds is that it provides an understanding of all results in the same framework: evolutionary stable strategies lead to an "optimal distribution" derived from the Ideal Free Distribution. This "optimal distribution" allows individuals to anticipate habitat variations and dispersal costs. We compare observations of natural populations with predictions of the model, which appears to be a good candidate to explain dispersal strategies in a variety of species.

05-03 Poster

WHO DO CHILDREN RESEMBLE MORE? CONSEQUENCES FOR PATERNAL INVESTMENT.

Alexandra Alvergne [1], Charlotte Faurie [1], Michel Raymond [1]

[1] *Université Montpellier II, Institute of Evolutionary Sciences, CC 065 Place eugène bataillon, 34095, Montpellier, FRANCE*

alvergne@isem.univ-montp2.fr

Father investment is facultatively expressed among humans and is related to paternity uncertainty. In order to direct their investment according to their offspring relatedness, fathers may use cues of paternity, such as facial or odor resemblance. Indeed, both traits have been found to be implied in social interactions through individual and family recognition in humans. In a context where phenotypic resemblance provides more paternity certainty and therefore more paternal care, children are expected to show a bias towards their father in their phenotype expression. However, the respective benefits of revealing or concealing paternity might differ depending on extra-pair paternity rate in the population. A study was conducted with 30 Senegalese families, and involved 2 children per family, aged from 2 to 7 years old (60 children in total). Each family member wore a T-shirt during one night and was taken in photograph. Recognition tests were performed by unrelated judges with each odor smelled 5 times and each face seen 50 times. Data on parental investment were collected, and the relation between resemblance and father investment was investigated.

05-04 Poster

BROOD PARASITISM AND SPATIAL RELATEDNESS IN THE BARNACLE GOOSE

Sofia Anderholm [1]

[1] *Gothenburg University, Zoology, Box 463, 40530, Gothenburg, Sweden*

sofia.anderholm@zool.gu.se

Alternative reproductive strategies raise intriguing evolutionary questions. Most examples studied are in males, but there are also a few in females. One example is conspecific nest parasitism, where a female (parasite) lays eggs in the nest of other females (hosts) of the same species and leave them for the host to take care of. This female strategy is found in insects, fish and more than 200 species of birds. If extra eggs impose a high cost on the host, a parasite does well in avoiding close relatives, whereas a small cost for the host may instead be overcome by inclusive fitness gains for closely related hosts and parasites. In species with precocial chicks, such as many waterfowl, the cost for the host may be low, and it is among these species that conspecific nest parasitism is most common. In addition, many waterfowl show strong female natal philopatry. Spatial relatedness may therefore have facilitated the evolution of conspecific nest parasitism through inclusive fitness gains. Relatedness between host and parasite has previously been found in for example goldeneye ducks and common eider ducks. Here we study relatedness between hosts and their parasites in a Baltic Sea population of barnacle geese using two molecular techniques, protein fingerprinting and microsatellite profiling. Preliminary results point to low or no relatedness between host and parasite in this population, and we found no within-island geographical pattern of relatedness. Possible reasons for these results are discussed.

05-05 Poster

EVOLUTION TO FISHERIAN SEX-RATIOS IN A COPEPOD WITH HERITABLE VARIATION FOR SEX-RATIO

Bradley R. Anholt [1], Leah Sauchyn [2]

[1] *University of Victoria, Biology, , Box 3020 STN CSC, V8N 2X5, Victoria, Canada*
[2] *University of Saskatchewan, Biological Sciences, Saskatoon, SA, Canada*

banholt@uvic.ca

The super-tidal copepod Tigriopus californicus has much more variable offspring sex ratios than expected if sex were chromosomally determined. While increased temperature will shift the clutch sex ratio to be slightly more male biased, offspring produce sex ratios similar to their parents. Cytological, and molecular investigations have eliminated Wolbachia and microsporidian meiotic drive agents. Antibiotic curing of clutches also has no effect on sex-ratio. In the field, sex ratios are extremely variable which suggests that there may be some adaptive explanation. We conducted a replicated selection experiment with populations derived from two sites. Cultures were initially established as either male and female biased. In all eight cases, sex ratio shifted towards 50:50 over the next 2 generations.

05-06 Poster

PARALLEL EVOLUTION OF SPECIES FLOCKS IN CRATER LAKE NEOTROPICAL CICHLIDS

Marta Barluenga [1, 2], Moritz Muschick [1], Walter Salzburger [1, 2, 3], Axel Meyer [1]

[1] *University of Konstanz, Department of Biology, Universitaetsstrasse 10, 78457, Konstanz, Germany*
[2] *University of Lausanne, Department of Ecology and Evolution, Le Biophore, 1015, Lausanne, Switzerland*
[3] *University of Basel, Department of Environmental Sciences, Vesalgasse 1, 4051, Basel, Switzerland*

Marta.BarluengaBadiola@unil.ch

Cichlid fishes are textbook examples for the process of adaptive radiation, rapid speciation and diversity of ecological adaptations and behaviors. Repeated evolution of similar strategies to cope with local environments appears as a common feature of distinct cichlid radiations. The Neotropical Midas Cichlid species complex (Amphilophus spp.) from the Great Lakes of Nicaragua, Central America, has repeatedly colonized several crater lakes in the area. Using different types of molecular markers –sequences of the mitochondrial control region and 15 microsatellites– combined with morphometric and ecological analyses, we identified parallel independent radiations in the Midas Cichlid species complex in several crater lakes in Nicaragua. These small-scale radiations involving 3-4 species in each crater lake contain some of the major ecomorphological types described in the more famous and species-rich East African cichlid radiations. Parallel ecological adaptations to alternative benthic and limnetic life styles evolved early after the colonization event, followed by more fine-scaled partitioning of the benthic area as an adaptation to alternative food resources.

05-07 Poster

THE SEX EXPRESSION IN LIFE HISTORY OF SEDGE CAREX SECALINA (CYPERACEAE)

Agnieszka Monika Bogdanowicz [1], Marlena Lembicz [1], Pawel Olejniczak [2], Julian Chmiel [1], Waldemar Zukowski [1]

[1] *Adam Mickiewicz University, Plant Taxonomy Department, 89 Umultowska Street, 61-614, Poznan, Poland*
[2] *Polish Academy of Science, Insitute of Nature Conservation, 33 Mickiewicza Street, 31-120, Krakow, Poland*

agab@amu.edu.pl

Carex secalina is a perennial monoecious sedge growing in tussocks and of iterative type of growth. It reproduces exclusively from seeds. In the life history of a sedge *Carex secalina* we have found out that a sex of spikes ranges from mono-zone unisex through two-zone bisexual–androgynous and gynaecandrous—to bisexual three-zone. In order to establish the life history of the species, 60 individuals were grown in the garden conditions. Each individual was a genet from one seed. The seeds were collected in two of the three populations of this species known in Poland. Statistically significant differences were found between the populations in the production of shoots with unisexual spikes and bisexual spikes. The average number of spikes per shoot differs between populations with unisexual spikes prevailing substantially. In the discussion an attempt is made to modify the present model of sex evolution of spikes in genera from the subgenus *Carex*. We have also indicated the usefulness of the traits of life history in recognition of the species evolution

05-08 Poster

ENERGY BUDGETS, POPULATION STRUCTURE, AND THE EVOLUTION OF MALE LIFE HISTORIES

David S. Boukal [1], Mikko Heino [1], Ulf Dieckmann [2]

[1] *Institute of Marine Research, Postboks 1870 Nordnes, 5817, Bergen, Norway*
[2] *International Institute for Applied Systems Analysis, Evolution and Ecology Program, Schlossplatz 1, 2361, Laxenburg, Austria*

davidb@imr.no

Many animals exhibit sexually dimorphic life histories. In particular, sexual size dimorphism (SSD) arises when growth trajectories differ between sexes, either before or after the onset of maturation. Fishes show the widest range of SSD, with male weights ranging from a tiny fraction to more than 12 times of that of females. In most cases, adult male fish are smaller, have a lower gonadosomatic index, and often exhibit a more truncated age distribution than females. This suggests that males and females acquire energy or use it in different ways, and that they might face different mortality risks. To study the evolution of SSD and its impact on a population's demographic composition, we use a sex-specific model of size-structured population with population-dynamical feedback and multiple, jointly evolving traits. These traits include, separately for both sexes, age/size at maturation and reproductive investment, as well as another abstract trait specific to males. This male trait can represent male-specific behaviour or morphology. We explore the evolutionary implications of alternative assumptions about what determines male fitness. Specifically, we show that adult male populations will evolve to consist of relatively few large 'macho' males monopolizing all females if male fitness is driven by a male trait that is proportional to acquired energy. By contrast, the existence of numerous small and early maturing 'non-macho' males requires male fitness to be determined primarily by the time males spend in reproductive activities. We discuss how our findings relate to previous results on SSD that did not explicitly consider sex-specific energy budgets and multiple evolving traits, and highlight directions for promising extensions of our approach.

05-09 Poster

THE FREQUENCY OF FITNESS PEAK SHIFTS IS INCREASED AT EXPANDING RANGE MARGINS DUE TO MUTATION SURFING.

Olivia J. Burton [1], Justin M. J. Travis [1]

[1] *University of Aberdeen, Zoology, Zoology Building, Tillydrone Avenue, AB24 2TZ, Aberdeen, UK*

olivia.burton@abdn.ac.uk

Dynamic ranges, either those that are invasive or shifting their range due to environmental change, are the focus of much recent interest in ecology, evolution and genetics. Studies (e.g. Klopfstein et al. 2006) have demonstrated that, at expanding range margins, single neutral mutations sometimes surf on the wave of advance reaching much higher frequency and spatial extent than would be expected in stationary populations. We extended this methodology to consider the genetic dynamics of 2 biallelic loci in populations shifting their ranges. In our initial population all individuals are genotype ab (the 'wildtype'). We incorporated epistatic interactions where a single mutation to a wildtype, at either locus (i.e. to aB or Ab), was deleterious but where the double mutant AB had higher fitness than the wildtype. The presence of double mutants during, and at the end of, each simulation was recorded for an expanding population. Simulations varying the fitness of single mutants were performed and the carrying capacity of each subpopulation, along with the number of offspring produced by each individual, was varied to assess their effects. In all cases simulations were repeated for stationary populations of equal size. Most significantly we demonstrated that double mutants were more likely to occur during range shifting than in stationary populations. This increased probability of peak shifting is associated with greater mean frequency of single mutants surfing on the edge of the range expanding population and therefore an increased likelihood that a double mutant will arise. The relative probability of fitness peak shifting in populations with stationary and dynamic ranges was highly dependent on the fitness of the single mutants. We argue that further work is required to assess the role of genetic architecture in driving the evolutionary dynamics of range expansion.

Klopfstein, S. et al. 2006. *Mol. Biol. Evol.* **23:** 482-490

05-10 Poster

INTEGRONS : AN EFFICIENT BACTERIAL ADAPTATION SYSTEM

Guillaume Cambray [1], Luis-Miguel Chevin [2], Didier Mazel [1]

[1] *Institut Pasteur, Genomes & Genetics, 25-28 rue du Docteur Roux, 75015, Paris, France*
[2] *Université Paris-Sud, Evolution et Systématique, Université Paris-Sud XI, Bâtiment 360, 91405 Orsay, France*

cambray@pasteur.fr

Integrons are complex genetic structures which are notably responsible for most of the antibiotics multiresistance phenotypes that threaten our control over pathogenic bacteria. The system maintains an unexpressed cassette array, which stands as a reservoir of potential genetic variation. Cassettes can then be randomly recombined at an expression site by a specific integrase. Overall this allows instantaneous expression of a potentially adaptive functions.

We model the evolution of recombination rate in a context of fluctuating selection. The integrase can be viewed as a modifier locus at which alleles are selected according to their effect on the cassettes expression. In the absence of deleterious mutations, we show that the mean recombination rate of a population tends to fit the environmental change rate. Biologically, this suggests that the most efficient strategy would be to control integrase expression so that recombination only occur when variations are needed. We demonstrate experimentally that the integrase expression is controlled by the SOS system, a well-known bacterial stress response. A further question is whether the accumulation of unexpressed deleterious mutations in the cassettes may result in long term deleterious consequences for the whole system.

This work highlights the importance of integrons as a major bacterial adaptation system through its effect on evolvavility.

05-11 Poster

THE POPULATION DYNAMIC CONSEQUENCES OF EVOLUTION OF AGE AND SIZE AT MATURATION IN RESPONSE TO HARVESTING IN AN EXPERIMENTAL MICROCOSM

Tom C. Cameron [1], Dan O'Sullivan [1], Alan Reynolds [1], Freda Marshall [2], Stuart B. Piertney [2], Tim G. Benton [1]

[1] *University of Leeds, Genetics, Ecology & Evolution, IICB, LC Miall building, LS2 9JT, Leeds, UK*
[2] *University of Aberdeen, Biological Sciences, Zoology building, Tillydrone Ave., AB24 2TZ, Aberdeen, UK*

t.c.cameron@leeds.ac.uk

The evolutionary responses of economically exploited populations (e.g. fisheries, trophy hunting etc) is a topic creating intense international debate at the present time. Here, I will present the first results from a long term (24 month, 30 generation) experiment attempting to separate the ecological and evolutionary effects of size-selective mortality on the life history of harvested populations in a laboratory system. Significant evolutionary responses in the life history are found (e.g. age/size at maturity), despite little change in population level genetic diversity (estimated from from AFLP-based analysis of proportion of polmorphic loci and nucleotide diversity). The population-dynamical consequences of these results are explored.

05-12 Poster

POST-INTRODUCTION SELECTION IN PHENOTYPIC TRAITS ENHANCES THE INVASION SUCCESS OF SENECIO PTEROPHORUS D.C. IN NE SPAIN

Lidia Caño [1], Josep Escarré [2], F. Xavier Sans [1]

[1] *University of Barcelona, Plant Biology, Diagonal 645, 08028, Barcelona, Spain*
[2] *Centre d'Écologie Fonctionnelle et Évolutiuve-CNRS, Dynamique de Systèmes Écologiques, 1919 Route de Mende, 34293, Montpellier, France*

lidiacano@ub.edu

Introduced species may become invaders as a result of rapid evolutionary changes associated with founding. Two not mutually exclusive selection pressures can affect exotics in the new range: release from native herbivores and new environmental conditions. We aimed to test this hypothesis with the invasive *Senecio pterophorus* D.C., a shrub native from South Africa and introduced in NE Spain *ca*. 40 years ago. In this area, its recent rapid spread may be indicative of a current range expansion after a lag time. We performed feeding choice bioassays and common garden experiments in the introduced range comparing 4 native and 4 invasive populations of *S. pterophorus*. Moreover, the main anti-herbivore compounds in this genus, the pyrrolizidine alkaloids, were analysed for each population.

The introduced populations showed higher concentrations of anti-herbivore chemical defences and were less palatable for a generalist herbivore than the native ones. In the common garden experiment, invasive Spanish populations displayed higher survival during drought periods and up to three times higher biomass than native South African populations, when growing under favourable conditions. Moreover the reproductive performance of the invasive populations was higher in all treatments. The results for leaf traits and chlorophyll fluorescence measurements suggested that the superior plastic performance of invasive populations was achieved through greater adaptive plasticity on ecophysiological traits. We suggest that interaction between ecological and evolutionary processes is favouring the invasion success of *S. pterophorus* by a rapid selection of traits relevant in the novel environment.

05-13 Poster

EVOLUTION AND MAINTENANCE OF ALTERNATIVE REPRODUCTIVE STRATEGIES IN BAG WORM MOTHS (LEPIDOPTERA: PSYCHIDAE)

Veronica Chevasco [1], Johanna Mappes [1], Jukka Jokela [2], Jelmer A. Elzinga [1], Alessandro Grapputo [3, 1]

[1] *University of Jyväskylä, Department of Biological and Environmental Sciences, P.O. Box 35, 40014, Jyväskylä, Finland*
[2] *EAWAG, Swiss Federal Institute of Aquatic Sciences and Technology, Department of Aquatic Ecology, Ûberlandstrasse 133, 8600, Dübendorf, Switzerland*
[3] *University of Padova, Department of Biology, Via Bassi 58 B, 35121, Padova, Italy*

vchevasco@gmail.com

A key question posed in evolutionary biology is why sex is maintained, but a satisfying explanation has not yet been found.

Asexuals only produce females and avoid the cost of sex. However, whereas sexual organisms generate higher genetic diversity through recombination, asexuals are considered to have low evolutionary potential due to the accumulation of mutations and the lack of genotypic diversity.

In Bag worm moths (Lepidoptera: Psychidae) both asexual and sexual lineages are found. Interestingly, in this group asexual reproduction is not clonal. Within a maternal family, only very few individuals have the same genotype which is likely the result of automictic thelytoky involving meiosis and recombination. Therefore, the maintenance of sex is a mystery in this group because sex is not related to increased genetic diversity.

05-14 Poster

SOCIAL INTERACTION AND DECAPOD CLAW MORPHOLOGY: THE CASE OF THE LONG-CLAWED SQUAT LOBSTER, MUNIDA RUGOSA

Thomas Claverie [1], Philip I. Smith [1]

[1] *University marine biological station, UMBSM, Isle of cumbrae, KA28 0EG, Millport, United kingdom*

thomas.claverie@millport.gla.ac.uk

Male decapods (crustaceans) have larger chelipeds than females and, in some species, a different cheliped shape. This sexual dimorphism has generally been attributed to males competing for access to females or to hold a territory. As with horns in ungulates or beetles, decapod chelipeds may be weapons for intra-sexual competition. Previous studies have demonstrated that cheliped morphology can be influenced by experience of prey handling during ontogeny. Consequently, a question arises whether social conditions can influence the development of cheliped morphology. This question was addressed using the squat lobster, *Munida rugosa*, a common galatheid on the west coast of Scotland that exhibits an unusual cheliped morphology with a suspected function in agonistic interactions. Most individuals have 'straight' chelae, in which the fingers of the claw are parallel and meet along their length. However, approximately 10% of large males have at least one 'arched' chela in which the fingers are curved and oppose only at their tips. The present study has shown that arched chelae are stronger and confer greater success in agonistic interactions than straight chelae. To assess whether the development of chela morphology depends on social conditions, the incidence of arched chelae has been compared in sub-populations (spatially separated, but assumed to be genetically similar) with different characteristics likely to be correlated with the intensity of male intrasexual competition, such as population density and sex ratio. It was expected that, depending on the degree of phenotypic plasticity, the incidence of arched chelae would be higher under conditions of more intense male competition for females.

05-15 Poster

KINSHIP-DEPENDENT DEFENCE IN THRIPS

Paulien J. A. De Bruijn [1], Martijn Egas [1], Arne Janssen [1], Maurice W. Sabelis [1]

[1] *Universiteit van Amsterdam, IBED, Kruislaan320, 1098SM, Amsterdam, The Netherlands*

bruijnp@science.uva.nl

When detecting a predatory mite, larvae of Western Flower Thrips (*Frankliniella occidentalis*) warn conspecifics by excreting a droplet of anal fluid containing alarm pheromones. This signal primes defensive responses in thrips larvae nearby. However, we found that the predatory mite is attracted by the alarm pheromone of its prey. Thus, by signalling danger to others, the thrips larvae put themselves at risk, but alert other thrips larvae nearby. This altruistic behaviour occurs in larvae of all sizes, yet it is more dangerous to small larvae, since they run a higher risk to be killed by a predatory mite.

To investigate the factors triggering altruism in thrips we tested whether thrips larvae respond differently to predatory mites (*Iphiseius degenerans*) when among kin than when among non-kin thrips. We observed that thrips produce alarm pheromone more frequently when among kin. To test whether kinship-dependent defence affects survival, we measured the mortality of thrips larvae in population experiments with various size-structured groups of thrips larvae, either in groups of kin or non-kin. Small thrips larvae experienced a lower predation risk in the presence of larger thrips larvae when they were kin. We also found a negative effect of kinship among thrips on the fitness of their predator: when kin, thrips larvae killed more predator eggs. We discuss the consequences of this defensive behaviour for the population dynamics of thrips and its predators.

05-16 Poster

SELECTION ON A QUANTITATIVE TRAIT IN AN AGE-STRUCTURED POPULATION FLUCTUATING IN NUMBER

Gerdien De Jong [1]

[1] *Utrecht University, Evolutionary Population Biology, Padualaan 8, 3584 CH, Utrecht, the Netherlands*

g.dejong@bio.uu.nl

Selection in an age-structured population has been well described if the population has a constant growth rate and is in stable age distribution. Both constant growth rate and stable age distribution must be rare in natural populations. What would be a good description of selection in a natural population?

The problem can be seen thinking of strong cohorts and weak cohorts in the population. Age-dependent selection will differ depending upon population composition. A selection differential or selection gradient over the total population might be estimated, but might differ between otherwise identical years just because of cohort composition of the population. Heritability estimates too might change with cohort composition.

I'll start from a one-locus two allele model specifying a quantitative trait in an age-structured population. Given the life-history as age-dependent survival and fecundity, both the change in genotypic mean of the quantitative trait and population number can be followed. The model can be used to specify how selection gradients are weighted averages of per cohort quantities, or whether parent-offspring estimates of heritability are consistently biased. The main use of the model is however in asking the effect of number fluctuations on the rate of change in the genotypic mean value of the quantitative trait, and of changes in selection strength on the trait influences number fluctuations.

05-17 Poster

DOES THE COST OF PHENOTYPIC PLASTICITY KEEP THE JACK OF ALL TRADES FROM BEING A MASTER OF ANY? AN EXPERIMENT ON CAENORHABDITIS REMANEI

S. Anaid Diaz [1], Jan Lindström [1], Dan Haydon [1]

[1] *University of Glasgow, Environmental and Evolutionary Biology, Glasgow, UK*

s.diaz-palacios.1@research.gla.ac.uk

Virtually all organisms live in a heterogeneous environment. It is commonly assumed that phenotypic plasticity is associated with environments variable in space and/or time, and that such a 'Jack of all trades' would do worse in a constant environment than a specialist would. However, such a cost of maintaining plastic responses in a constant environment has not been demonstrated experimentally. The purpose of my project is to address this question by using long-term selection experiments on a gonochoristic nematode species (*Caenorhabditis remanei*). Initially, I will maintain lines of worms for 50 generations under two temperature regimes: constant temperature (mean 15±1°C) and fluctuating environment with the same mean but temperature fluctuating between 5 and 25°C every 12 hours. After 50 generations in each environment, populations will be transposed between these environments. Specific life-history traits (age-specific and total fecundity, maturation time and mortality) will be assayed prior to and after the initial selection experiment. Comparison of these traits across the environments will enable me to determine if maintenance of plasticity is costly in a constant environment, and if specialisation to a constant environment carries a cost when transferred to a fluctuating environment. Preliminary results of this experiment will be presented and discussed.

05-18 Poster

GENETIC DIVERGENCE IN THE ATLANTIC-MEDITERRANEAN MONTAGU'S BLENNY CORYPHOBLENNIUS GALERITA (LINNAEUS 1758) REVEALED BY MOLECULAR AND MORPHOLOGICAL CHARACTERS

Vera S. Domingues [1], Claudia Faria [2], Sergio Stefanni [3], Ricardo S. Santos [3], Alberto Brito [4], Vitor C. Almada [2]

[1] *ISPA and Univ. Azores, UEE and DOP, Rua Jardim Tabaco 34, 1149, Lisbon, Portgal*
[2] *ISPA, UEE, Portugal*
[3] *Univ. Azores, DOP, Portugal*
[4] *Univ. La Laguna, Biologia Animal, Spain*

v_domingues@yahoo.com

We examined Atlantic and Mediterranean populations of the mall intertidal fish *C. galerita* to assess levels of genetic divergence across populations and to elucidate historical and contemporary factors underlying the distribution of the genetic variability. We analyze mitochondrial and nuclear marker and morphological measurements. The combined dataset clearly supports the existence of two groups of *C. galerita*: one in the Mediterranean and another in the northeastern Atlantic. The latter group is subdivided in two subgroups: Azores and the remaining northeastern Atlantic locations. Divergence between the Atlantic and the Mediterranean can be the result of historical isolation between the populations of the two basins during the Pleistocene glaciations. Present day barriers such as the Gibraltar Strait or the "Almeria-Oran jet" are also considered. Our results show no signs of local extinctions during the Pleistocene glaciations, namely at the Azores, and contrast with the biogeographical pattern that has been observed for Atlantic-Mediterranean warm water species. This study is one of the first to combine morphological and molecular markers (mitochondrial and nuclear) with variable rates of molecular evolution to the study of the relationships of the Atlantic and Mediterranean populations of a cool water species.

05-19 Poster

DYNAMIC BALANCE BETWEEN OPPOSING NATURAL AND FISHERY SELECTION DRIVES RAPID LIFE HISTORY EVOLUTION

Eric Edeline [1], Stephanie M. Carlson [2], Leif C. Stige [1], Ian J. Winfield [3], Janice M. Fletcher [3], J B. James [3],
Thrond O. Haugen [4], L A. Vøllestad [1], N C. Stenseth [1]

[1] *University of Oslo, CEES, P.O. Box 1066 Blindern, 0316, Oslo, Norway*
[2] *School of Aquatic and Fishery Sciences, Seattle, USA*
[3] *Centre for Ecology & Hydrology, Lancaster, UK*
[4] *NIVA, Oslo, Norway*

eric.edeline@bio.uio.no

Lack of demographic recovery following relaxation of fishing could result from hardly reversible evolution to slower somatic growth, earlier maturity and increased reproductive effort. Here in contrast we show in Windermere pike (*Esox lucius*) that decreasing harvest rate induced rapid energy reallocation from reproduction to somatic growth. Linear (long term) trend for 13,942 individuals from 1945 to 1995 show that pike somatic growth increased, most likely due to intensified cannibalism. Nonlinear (short term) changes show that increase in somatic growth was tightly connected to the stepwise relaxation of the fishing pressure. This result provides evidence that fishery selection was impeding readjustment to the moving natural adaptive optimum. Additionally, we estimated changes in the intercept and slope of the reproductive investment/length reaction norm for 3,092 females captured after the fishing pressure dropped, taking into account the effects of age and surplus energy gained prior to capture. Reproductive investment decreased in egg-number (but not egg-size), and investment now occurs at a larger body length. The age-specific amplitude of these changes matched with the age-specific fishing pressure, suggesting that reduced investment was an adaptive response to increased life-expectancy. Our results strongly support to the view that life-history evolution in exploited fish stocks results from a dynamic balance between opposing natural and fishery selections.

05-20 Poster

HOW DO HARVEST-INDUCED LIFE-HISTORY CHANGES INFLUENCE POPULATION DYNAMICS AT LOW ABUNDANCE?

Katja Enberg [1], Erin S. Dunlop [2], Mikko Heino [2], Ulf Dieckmann [3]

[1] *Institute of Marine Research, P.O. Box 1870 Nordnes, 5817, Bergen, Norway*
[2] *Bergen, Institute of Marine Research, P.O. Box 1870 Nordnes, 5817, Bergen, Norway*
[3] *International Institute for Applied Systems Analysis, Evolution and Ecology Program, Schlossplatz 1, 2361, Laxenburg, Austria*

katja.enberg@bio.uib.no

Humans strongly affect the demography of harvested populations. These demographic effects include decreased overall population abundance and truncated age- and size-structure. On top of these, increased mortality might also cause changes in life-history traits, thus further affecting the genetic and phenotypic structure of exploited stocks. Such evolutionary changes have been suggested to contribute to widespread trends towards fish maturing at earlier ages and smaller sizes. Furthermore, these life history changes might also decrease the reproductive potential of the population.

Population dynamics at low population abundances can show unexpected nonlinearities. If reproduction of individuals in the population is not successful at low population sizes as a result of, for example, inability to find mates or form sufficient breeding aggregations, the population growth rate might become negative. The probability of reaching low enough abundances to observe Allee-effects increases when harvesting pushes the population towards smaller sizes.

In this work, we study the interplay between different population renewal patterns and we examine the role of dynamics at low population sizes. We use an individual-based eco-genetic model with multiple evolving traits (maturation schedule, reproductive investment, and intrinsic growth capacity) in order to investigate the interplay of harvest-induced evolution and population renewal processes. Our results have implications for resource management and conservation, especially with respect to the development of biological reference points used for managing exploited fish stocks.

05-21 Poster

THE POTENTIAL GENETIC CONSEQUENCES OF NON-NATURAL MATING IN BROWN TROUT

Guillaume Evanno [1], Rudolf Müller [2], Claus Wedekind [1]

[1] *University of Lausanne, Department of Ecology and Evolution, Biophore, 1015, Lausanne, Switzerland*
[2] *Swiss Federal Institute for Environmental Science and Technology (EAWAG), Fish Ecology and Evolution, 6047, Kastanienbaum, Switzerland*

guillaume.evanno@unil.ch

Salmonids are usually managed by supportive breeding, i.e. the artificial breeding of adults and subsequent release of offspring into the wild. Supportive breeding has often proven beneficial for endangered populations but it may, under some conditions, cause detrimental genetic effects because of the enforced random mating of breeders. Mating in the wild is probably never random: intra-sexual selection is usually important in salmonids, and good-genes models of sexual selection predict that females choose males of superior genetic quality. Here we used artificial fertilizations and a quantitative genetics design in Brown trout (Salmo trutta), a species with no parental care, to analyze male genetic quality measured by two major components of fitness: embryo and juvenile survival. Embryo survival was recorded in the laboratory under controlled conditions. We then released the hatchlings into a natural river, caught the surviving juveniles 20 months later, and used genetic assignment to identify their parents. We found significant maternal and paternal effects on embryo survival. In contrast, juvenile survival was significantly affected by sire effects but not by dam effects. We use our findings to compare the genetic effects of different mating scenarios: (i) perfect random mating (as in state-of-the art hatcheries), (ii) male reproductive success linked to size, i.e. a trait linked to dominance in intra-sexual selection, and (iii) perfect female choice, assuming that females could optimize offspring viability. We found a significant potential of sexual selection to improve offspring viability in next generations.

05-22 Poster

COOPERATIVE BREEDING AND THE EVOLUTION OF THE HUMAN FAMILY

Charlotte Faurie [1], Alexandra Alvergne [1], Michel Raymond [1], Andrew F. Russell [2], Virpi Lummaa [2]

[1] *University of Montpellier, Institute of Evolutionary Sciences, CC 065 - pl. E. Bataillon, 34095, Montpellier, France*
[2] *University of Sheffield, Derpartment of Animal and Plant Sciemces, Western Bank, S102TN, Sheffield, United Kingdom*

faurie@isem.univ-montp2.fr

Apparently paradoxical breeding strategies exist where individuals appear not to compete but to cooperate, helping to rear offspring that are not their own. Species in which individuals exhibit such breeding strategies are known as cooperative breeders, and are most famous in social insects, but are also common in birds and mammals. In humans, as in several other mammal species, older siblings may act as helpers by providing direct care to children, or by assisting the parents in their activities. We conducted a study of cooperative behaviours exhibited by brothers and sisters, in a rural population in Senegal, where modern contraception methods are absent so that family size can be considered as "natural". Firstly, we investigated whether the presence and number of older brothers and sisters, and their cooperative behaviours, influence child condition. Helping behaviours (help provided to the parents for the care of younger siblings) were assessed through interviews given to the parents. Child condition was estimated by body size, arm girth, health status, school attendance, and stress level, as measured by cortisol concentration in saliva samples (stress hormone). Secondly, we studied how familial and social factors influence helping behaviours, and how this can be mediated by variations in cortisol levels. Finally, we conducted an experiment in order to investigate how hormones related to helping in other cooperative mammals can explain any differences in helping behaviour found between family members. The cortisol response to playbacks of baby cries was compared to the cortisol response to a control sound, and the difference was analyzed in relation to sex, age, socio-economic status, number of siblings, birth order, and helping behaviour. The results and their consequences for the evolution of the family are discussed.

05-23 Poster

GENETIC CHARACTERIZATION OF A BOVINE HERD OF THE BOS TAURUS BREED PÉ-DURO FROM PIAUÍ STATE, NORTHEASTERN BRAZIL, BASED ON MICROSATELLITES

Ana P. F. Oliveira [1], Maria A. C. Lara [2], Marcos M. Miretti [3, 4], Eucleia P. B. Contel [1]

[1] *Faculdade de Medicina de Ribeirão Preto-USP, Departamento de Genética, Avenida Bandeirantes 3900, 14049-900, Ribeirão Preto-SP, Brazil*
[2] *Instituto de Zootecnia, Rua Heitor Penteado, 56, 13460-000, Nova Odessa-SP, Brazil*
[3] *Faculdade de Ciências Agrárias e Veterinária, Departamento de Tecnologia, Jaboticabal-SP, Brazil*
[4] *Wellcome Trust Sanger Institute, Cambridge, United Kingdom*

anapfo@usp.br

The objective of this study was to characterize genetically a cattle population of the *Bos Taurus,* breed Pé-duro (n=126) from Piauí State, Northeastern Brazil. We examined heterozygosity, polymorphism information content (PIC), allelic frequency and genetic diversity, inbreeding coefficient (f) and Hardy-Weinberg equilibrium based on six microsatellites loci, SPS115, BM1824, BM2113, BMS4049, TGLA122 and ETH225. A total of the 57 alleles were identified, the largest genetic diversity was verified in the locus TGLA122 (91,3%), the smallest in the locus BMS4049 (45,5%). The mean expected heterozygosity (72,8%) and mean observed heterozygosity (57,8%). PIC calculated for each marker exceeded 0,50, except for the BMS4049 locus (43%) and the mean PIC in Pé-duro breed is (70,3%). However we also observed a significant (f) for this population ($f = 0,207$ $P < 0,01$) and deviations from Hardy-Weinberg equilibrium in all loci analyzed. Therefore, the conservation of this Pé-duro Brazilian breed is important because it constitutes a genetic background which checks adaptation to the unfavorable environmental conditions of northeastern region, Brazil, and for more than 400 years it helped to write the history this country. Besides, the its genetic characterization is fundamental because provides information for genetic improvements programs for future livestock.

Keywords: Pé-duro, *Bos taurus*, microsatéllites, genetic characterization, conservation.

05-24 Poster

INSIGHTS INTO THE ADAPTIVE RADIATION OF AFRICAN WEAKLY ELECTRIC FISH (GENUS: CAMPYLOMORMYRUS): EVIDENCE FOR SYMPATRIC SPECIATION FROM A MULTIDISCIPLINARY APPROACH

Philine G. D. Feulner [1], Frank Kirschbaum [2, 3], Ralph Teidemann [4]

[1] *University of Potsdam, Institute of Biochemestry and Biology, Karl-Liebknecht-Str. 24-25, 14476, Potsdam, Berlin*
[2] *Humboldt University Berlin, Institute of Animal Sciences, Philippstr. 13, 10099, Berlin, Germany*
[3] *Institute of Freshwater Ecology and Inland Fisheries, Depatrment of Biology and Ecology of Fishes, Müggelseedamm 310, 12587, Berlin, Germany*
[4] *University of Potsdam, Institute of Biochemestry and Biology, Karl-Liebknecht-Str. 24-25, 14476, Potsdam, Germany*

feulner@uni-potsdam.de

Within the osteoglossomorpha the African weakly electric fish or mormyrids are by far the most species-rich taxon. They use their Electric Organ Discharge (EOD) for active electrolocation and communication. Interestingly, the mormyrid genus *Campylomormyrus* contains a huge variety of different EOD waveforms. To shed light on the speciation processes within this genus, we have sampled 106 individuals near Brazzaville (Congo Basin). We adopted a multidisciplinary approach, combining a variety of molecular markers with geometric morphometrics, and monitoring of diversification in the EOD waveforms to build up the first convincing phylogenetic hypothesis for *Campylomormyrus*. Sequences of mitochondrial and nuclear genes consistently identified at least five reciprocally monophyletic clades occurring in sympatry. Assignment tests and pairwise F_{ST} values based on 16 microsatellite loci corroborated these results. Morphometric analyses showed that the major source of differentiation among clades resides in traits correlated with the feeding ecology. These results, along with those on adult EODs, suggest that *Campylomormyrus* underwent an adaptive radiation, possibly in sympatry. This was triggered by sexual selection via assortative mating due to differences in EODs and was associated with divergent selection of ecologically important morphological traits.

05-25 Poster

REGION-SPECIFIC SIGNALS OF SELECTION IN THE AVPR1A GENE IN MAMMALS

Sabine Fink [1], Laurent Excoffier [1], Gerald Heckel [1]

[1] *University of Bern, CMPG, Zoological Institute, Baltzerstrasse 06, 3012, Bern, Switzerland*

sabine.fink@zoo.unibe.ch

Regulatory important structures like hormone receptors evolve under functional constraints and are thus expected to be subjects to purifying selection. Some regions of a gene coding for functional units can nevertheless be targets of positive selection and may thus result in phenotypic adaptations. The arginine-vasopressin 1a receptor in the brain has been identified as a key determinant for phenotypic variation in social behavior in *Microtus* voles and other mammals. In this study, we examine genetic variation in the *arginine-vasopressin receptor 1a (avpr1a)* gene across a range of mammal taxa in order to determine the influence of non-neutral processes for the evolution of this receptor. We address potential functional consequences by contrasting non-synonymous variation at this locus with life history traits (e.g. mating system) and geographic variation. Analysis of the first exon of the gene revealed regions with a comparatively high rate of change which showed also evidence for positive selection on particular sites. Genetic variation within the *Microtus* genus involves deletions or insertions of amino acids in the protein coding region of the gene, the replacement of amino acids with radically different physicochemical properties, and the presence of distinct protein variants within individuals. These results are discussed in regards to functional constraints and the occurrence of adapted receptor phenotypes.

05-26 Poster

ASSOCIATIONS OF COLOUR POLYMORPHISM WITH RANGE SIZE, NICHE BREADTH AND CONSERVATION STATUS AMONG AUSTRALIAN REPTILES

Anders Forsman [1], Viktor Åberg [1]

[1] *University of Kalmar, School of Pure and Applied Natural Sciences, 391 82, Kalmar, Sweden*

Anders.Forsman@hik.se

We evaluate predictions concerning the evolutionary and ecological consequences of chromatic polymorphisms. Previous endeavours have aimed primarily at identifying conditions that promote the evolution and maintenance of polymorphisms. However, the polymorphic condition may also influence important processes at the population level. We consider here the proposition that populations that consist of alternative colour- or ecomorphs with co-adapted gene complexes will utilize more diverse resources, and display higher rates of colonization success, population persistence and range expansions, while being less vulnerable to range contractions and extinctions, compared with monomorphic populations. To evaluate this proposition we perform pair-wise comparative analyses based on information for 323 species of Australian lizards and snakes. We find that species with variable colour patterns have larger ranges, utilize a greater diversity of habitat types and are underrepresented among species currently listed as threatened. These results support the notion that colour polymorphism may play a serviceable part in the evolutionary life of individual species.

05-27 Poster

ADAPTIVE DEVELOPMENTAL PLASTICITY IN GROWING NESTLINGS: SIBLING COMPETITION INDUCES DIFFERENTIAL GAPE GROWTH

Diego Gil [1], Elena Bulmer [1], Patricia Celis [2], Isabel Lopez [1]

[1] *Museo Nacional de Ciencias Naturales, Ecologia Evolutiva, Jose Gtez Abascal 2, 28200, Madrid, Spain*
[2] *University of St Andrews, Biology, KY16, Fife, UK*

dgil@mncn.csic.es

Sibling competition has been shown to affect growth rates in birds. However, little is known on the effect of this selective pressure on developmental plasticity. We would expect that structures that are used for sibling competition, such as the gape of altricial nestlings, should present an enhanced development when competition for resources is high. We conducted an experiment in the spotless starling (Sturnus unicolor), in which nestlings were cross-fostered to nests with different levels of sibling competition. We predicted that nestlings subject to higher levels of sibling competition should develop larger gapes than control birds. We found that growth of most morphological traits was reduced in nests with intense sibling competition, whereas gape width remained unaffected. At the end of the nestling period, experimental nestlings had wider gapes than controls. In a further correlative study, we found that nestling gape width increased when feeding conditions worsened and body size decreased. These patterns could either be due to increased growth of gape flanges or to delayed maturation. Our results show that birds can invest differentially in the development of organs during growth, and that the growth of organs used in sibling competition is given priority over structural growth. Adaptations such as these may shift the final size of adult traits, thus pushing away organisms from naturally selected optima.

05-28 Poster

WHEN FECUNDITY DOES NOT EQUAL FITNESS: EVIDENCE OF A QUANTITY-QUALITY TRADE-OFF IN PRE-INDUSTRIAL HUMANS

Duncan O. S. Gillespie [1], Andrew F. Russell [1], Virpi Lummaa [1]

[1] *University of Sheffield, Animal & Plant Sciences, Western Bank, S10 2TN, Sheffield, UK*

d.gillespie@sheffield.ac.uk

Lack (1954) suggested that individual fitness is maximised by optimising (not maximising) the number of offspring produced, because a trade-off exists between quantity and quality. However, tests of this idea in wild animals are often conducted using single breeding events and not lifetime reproduction, and offspring quality is measured as survival, not reproductive success. Additionally, comprehensive tests of quantity-quality trade-offs using adequate fitness measures, and their modification by resource availability, are difficult in wild animals because of the paucity of records of dispersers' reproductive success and measures of habitat quality. Here we use 150 years of human life- history data from Finns living in conditions of natural fertility and mortality to investigate: 1) evidence of a quantity-quality trade-off using grandchildren numbers produced as a fitness estimate, 2) how this trade-off is modified by habitat quality and social class, and 3) determine how this trade-off is mediated. We show that there is good evidence for a quantity-quality trade-off in lifetime reproduction for pre-industrial Finns and that this is strongest in low quality habitat or with low access to resources due to being poor. We demonstrate that the major factor behind the quantity-quality trade-off is differential offspring survival and discuss the potential selection on fecundity at different levels of resource availability.

05-29 Poster

INSERTION OF A BARI1 TRANSPOSON ASSOCIATED WITH GENES INVOLVED IN JUVENILE HORMONE METABOLISM

Josefa Gonzalez [1], J. Michael Macpherson [1], Dmitri A. Petrov [1]

[1] *Stanford University, Biological Sciences, 371 Serra St, 94305, Stanford, USA*

jgonzalp@stanford.edu

Many transposable elements (TEs) in *Drosophila melanogaster* are deleterious due to harmful effects of ectopic recombination among dispersed TE copies. Because of this particular TEs are unlikely to reach high population frequencies unless they either fail to participate in ectopic recombination or, alternatively, if this TE produces an adaptive effect. Screening for unusually frequent TEs resulted in the discovery of an insertion of a Doc element that leads to pesticide resistance. Here we describe the analysis of a highly frequent insertion of a Bari1 element that is inserted in the 0.8 kb region between the Juvenile hormone epoxide hydrolase 2 (Jheh2) and the Jheh3 gene. Jheh2 and Jheh3 are involved in Juvenile Hormone (JH) metabolism. We sequenced the regions flanking the Bari1 element and we found signatures of positive selection. We also obtained population genetics data of the neighbouring genes in *D. melanogaster*, *D. simulans* and *D. yakuba* and analyzed the molecular evolution of these genes in these three species and also in the other Drosophila species available. To understand the molecular and phenotypic effects of this insertion we used repeated backcrosses to generate two strains with largely identical genetic backgrounds except for the presence/absence of the element. These strains were used to analyze the effects of the Bari1 insertion on the expression of Jheh genes during *D. melanogaster* development.

05-30 Poster

DEMOGRAPHIC EFFECTS OF INCREASING TEMPERATURES ON THE ZEBRA MUSSEL DREISSENA POLYMORPHA: A SIMULATION STUDY.

Eva M. Griebeler [1], Alfred Seitz [1]

[1] *University of Mainz, Department of Zoology, Saarstr. 21, 55099, Mainz, Germany*

em.griebeler@uni-mainz.de

Zebra mussels (*Dreissena polymorpha*, Pallas, 1771) have had an unprecedented success in colonizing European and North American waters under strongly differing water temperature regimes. Thus, the mussel is an excellent model of a species which is able to cope with increasing water temperatures expected under global change. We study three principle scenarios for its successful survival under rising temperatures: (1) no adaptation to future thermal conditions is needed, existing performance is sufficient, (2) a shift (adaptation) towards higher temperatures is required; or (3) a broadening of the range of tolerated temperatures (adaptation) is needed. To derive which alternative might enable its future survival we developed a stochastic individual-based model. It describes the demographic growth of *D. polymorpha* and is a day-degree model which is determined by ambient water temperature. Daily temperatures are generated based on long-term data of the River Rhine. Predictions under temperature conditions as recently observed for this river that are made for the phenology of reproduction, the age distribution and the shell length distribution conform with field observations. Our simulations show that temporal patterns in the life-cycle of the mussel will be altered under rising temperatures. In all scenarios spawning started earlier in the year and the total reproductive output of a population was dominated by the events later in the spawning period. For maximum temperatures between 20 and 26 °C no thermal adaptation of the mussel is needed (scenario 1). No extinctions and stable age distributions over generations were observed in scenario 2 for all maximum temperatures studied. In contrast, no population with a fixed range of tolerated temperatures survived in scenario 3 with high maximum temperatures (28, 30, 32 °C). Age distributions showed an excess of 0+ individuals which resulted in an extinction of the population for several thermal ranges investigated.

05-31 Poster

SOCIAL CONSTRAINTS LIMIT DISPERSAL AND SETTLEMENT DECISIONS IN A GROUP-LIVING BIRD SPECIES

Michael Griesser [1], Madgalena Nystrand [2], Sönke Eggers [2], Jan Ekman [2]

[1] *Sheffield University, Animal and Plant Sciences, S102TN, Sheffield, UK*
[2] *Uppsala University, Population Biology, 75236, Uppsala, Sweden*

michael.griesser@gmail.com

Dispersal is a fundamental process affecting the genetic structure of populations, speciation and extinction. Nevertheless, our understanding of the evolution of dispersal is limited by our paucity of knowledge on dispersal decisions at the individual level. We investigated the effect of interactions between residents and juvenile dispersers on dispersal and settlement decisions in Siberian jays (Perisoreus infaustus). In this group-living bird species, some offspring remain on the parental territory for up to three years (retained juveniles) while other offspring disperse promptly after independence (dispersers). Retained juveniles constrained settlement decisions of dispersers by aggressively chasing dispersers off their territory, thus preventing them from settling. As a result, dispersers mainly settled in groups without retained juveniles. Experimental removal of male breeders during the dispersal period demonstrated that dispersers were unable to settle in high quality breeding openings, which were instead filled by older non-breeding residents. Rather, dispersers immigrated into groups where they became subordinate group members, queuing for a breeding opening. Moreover, dispersal did not inflict a cost through increased mortality. While breeders benefit from having immigrants in their group as replacement mates upon death of own mate, immigrants inflicted a fitness cost to breeders. The presence of immigrants increased the rate of conflicts during the breeding season which negatively affected nestling condition. The results of this study highlight that resident individuals constrain both dispersal and settlement decisions of dispersers. Social interactions between residents and dispersers can thus be an essential factor to understand the evolution of dispersal.

05-32 Poster

CAN THE EVOLUTION OF BOLDNESS FACILITATE RAPID RANGE EXPANSION BY INVASIVE ORGANISMS?

Mattias Hagman [1], Peter A. Biro [2], Benjamin L. Phillips [1], Richard Shine [1]

[1] *The University of Sydney, School of Biological Sciences, Australia*
[2] *University of Technology, Department of Environmental Science, and Institute for Water and Environmental Resource Management, Sydney, Australia*

mhag8451@mail.usyd.edu.au

Selective forces at an invasion front may favour individuals that are highly dispersive and able to exploit novel environments – and hence tend to be “bold” in numerous contexts rather than “shy”. The invasion process likely selects for bolder individuals, because these will exhibit more dispersive behaviour even in the face of risk. To test this hypothesis we examined activity levels in cane toad (*Chaunus* [*Bufo*] *marinus*) tadpoles from invasion-front versus “old” (long-established) populations. Previous studies provide clear evidence that adult cane toads have been selected for increased dispersal ability during their invasion of northern Australia, but tadpoles are not the primary dispersal phase of cane toads. Although there has been no direct selection on dispersal in tadpoles, we may still expect to see heightened activity levels (and boldness generally) in tadpoles from the invasion-front, because of indirect selection operating via the adult life-history stage. Our results from tadpoles that were produced, raised and tested in a laboratory support this prediction. Tadpoles from invasion-front populations had consistently higher activity levels (both in the presence and absence of risk) than did tadpoles from older populations, matching patterns seen in adult toads.

05-33 Poster

THE MAINTENANCE OF HERITABLE VARIATION THROUGH SOCIAL COMPETITION

Ed Harris [1], Jason Wolf [1]

[1] *University of Manchester, Faculty of Life Sciences, Michael Smith Building, M21 9PT, Manchester, UK*

ed.harris@manchester.ac.uk

The maintenance of heritable genetic variation for fitness related traits is a pre-eminent problem in evolutionary biology. Paradoxically, these traits often exhibit significant amounts of heritable variation despite the expectation that selection should quickly erode such variation. Several mechanisms have been suggested to contribute to the evolutionary maintenance of genetic variation, yet none has provided a general explanation for the long-term persistence of heritable variation under constant selection. Here we describe a simple mechanism where social competition results in the maintenance of heritable variation for fitness related traits. We demonstrate this mechanism using a simple genetic model with two main biological assumptions: the expression of a trait depends upon success in social competition for limited resources; and competitive success is non-additive, such that the success of a genotype depends on the genotypes that it competes against. We find that such social competition generates heritable (additive) genetic variation for “competition dependent” traits and that selection on these traits results in complex long-term allelic variation due to the concerted co-evolution of the social environment with the effects of alleles. Thus, our results provide a novel mechanism for the generation and maintenance of heritable variation in natural populations.

05-34 Poster

ADAPTATION OF DROSOPHILA MONTANA POPULATIONS TO DIFFERENT ENVIRONMENTAL CONDITIONS AT THE GENETIC AND TRANSCRIPTIONAL LEVEL

Anneli Hoikkala [1], Maaria Kankare [1], Jarkko Routtu [1]

[1] *University of Jyväskylä, Department of Bio- and Environmental Sciences, P.O.Box 35, 40014, Jyväskylä, Finland*

anhoikka@bytl.jyu.fi

The majority of information on adaptation in wild populations is from DNA markers and/or quantitative characters, while the connection between the genes and environmental signals is still poorly understood. We will trace this connection in *Drosophila montana,* a species of the *D. virilis* group distributed around the northern hemisphere. The phenotypic divergence among American, Canadian and Finnish populations of this species in male wing, song and genital characters is high and it does not coincide with the extent of genetic divergence of populations, suggesting that the phenotypic characters are not evolving neutrally. Northern populations survive through the harsh winter conditions in photoperiod reproductive diapause, while the flies in our samples from southern populations lack this ability. The genetic basis of population divergence in morphological, physiological and behavioural traits is being studied by classical crossing and mapping schemes as well as by studying sequence variation and expression in genes found to affect the studied traits in *D. melanogaster*. We have designed microarray probes for *D. montana* for several genes (about 120 at present) known to affect reproductive diapause, circadian clock, response to cold, heat and light and courtship behaviour in the genetic model species *D. melanogaster* and in future we plan to add more genes to this array. With the aid of the 'candidate gene microarray' we will trace differences in genes likely to be responsible for the divergence of *D. montana* populations in traits important in survival, overwintering ability and reproduction of the flies at a functional level.

05-35 Poster

FEMALE MATE CHOICE DRIVES MALE DISPERSAL IN A SOCIAL MAMMAL

Oliver P. Höner [1], Bettina Wachter [1], Marion L. East [1], Jürgen W. Streich [1], Kerstin Wilhelm [1], Terry Burke [2], Heribert Hofer [1]

[1] *Leibniz Institute for Zoo and Wildlife Research, Evolutionary Ecology, Alfred-Kowalke-Str. 17, 10315, Berlin, Germany*
[2] *University of Sheffield, Department of Animal and Plant Sciences, Western Bank, S10 2TN, Sheffield, UK*

hoener@izw-berlin.de

We investigated whether male-biased dispersal in social mammals is driven by avoidance of male mating competition, resource competition, inbreeding or by female mate choice. For this purpose, we analysed long-term demographic data from eight social groups ('clans') of spotted hyenas (*Crocuta crocuta*), and determined female mate preferences and fitness benefits of decisions made by males using microsatellite profiling of 426 offspring. Females avoided mating with males that were members of their clan when they were born and preferred sires that immigrated or were born into their clan after their birth. Furthermore, young females preferred short-tenured sires and older females preferred longer-tenured sires. Given these female mate preferences, males would be expected to initiate their reproductive career in the clan containing the highest number of young females. Males conformed to this expectation and, as a consequence, 11% of males started their reproductive career in their natal clan and 89% of males dispersed. Males that initiated their reproductive career in the clan containing the highest number of young females had a higher long-term reproductive success than males that did not. There was no evidence that males dispersed to avoid male mating competition, resource competition or breeding with close relatives. We conclude that female mate choice represents a sufficient cause for the evolution of sex-biased dispersal in spotted hyenas. The observed female preferences were simple mate choice rules that neither discriminate against close kin or natal males nor favour immigrant males but instead are based on simple time-based discrimination cues that lead to a high level of male dispersal and radically reduced the chance of costly inbreeding for females. In such systems, the extent of male dispersal depends on the demographic structure in breeding groups (including the natal group), rather than genetic relatedness between males and females.

05-36 Poster

MANAGEMENT OF THE URBAN PIGEON: ECOLOGICAL AND ANTHROPOLOGICAL ASPECTS

Gwenaël Jacob [1], Emmanuelle Baudry [1], Didier Lapostre [2], Catherine Dehay [2], Pascale Beauvois [2], Patrick Mur [3], Romain Julliard [4], Véronique Servais [5], Anne-Caroline Prevot-Julliard [1]

[1] Université Paris-Sud XI, Dept d'Ecologie, Systématique et Evolution - UMR 8079, Bât. 362, 91405, Orsay, France
[2] AERHO, 1, rue Malot, 93100, Montreuil, France
[3] LPO Île de France, 62, rue Bargues, 75015, Paris, France
[4] Muséum National d'Histoire Naturelle / CRBPO, Dept d'Ecologie et Gestion de la Biodiversité - UMR 5173, 55, rue Buffon, 75005, Paris, France
[5] Université de Liège, Dept des Arts et Sciences de la Communication, Place du 20 août, Bât. A1, 4000, Liège, Belgium

gwenael.jacob@u-psud.fr

Feral pigeons *Columba livia* are nowadays present in most large cities, where they benefit from nesting sites in large buildings and from food provided by humans. As a consequence of their prevalence in towns pigeons are also considered an urban pest. Several, sometimes conflicting, actors are involved in the management of urban populations of the pigeon. The aim of our project is to establish recommendations for the management of the pigeon in urbanized areas that do not conflict with the perception of nature by citizens. For this, we combine the expertise of ecologists, anthropologists and nature conservation associations.

In France, dovecotes have been built as a mean to regulate pigeon populations and, thus, improve the public attitude towards pigeons. However, the efficiency of dovecotes has not been proven.

I will present our study on individual behavior and population dynamics within a dovecote study. We also investigated how the genetic structure of the population of the feral pigeon in Paris relates to the distribution and abundance of the species since the last century.

The feral pigeon is a valuable biological system to investigate the relationship between humans and nature.

05-37 Poster

DIFFERENT SPECIALISATION AMONG COSELY RELATED SPECIES RESULTS IN CONTRASTING POPULATION RESPONSES TO PLEISTOCENE GLACIAL ADVANCES - COMPARATIVE DEMOGRAPHIC ANALYSIS OF ANTARCTIC SHELF FISHES

Karel Janko [1], Guillaume Lecointre [2], Art DeVries [3], Craig Marshall [4]

[1] Institute of Animal Physiology and Genetics, Czech Academy of Sciences, Dept. Fish Genetics, Rumburska 89, 22721, Libechov, Czech republic
[2] National Museum of Natural History, 43 rue Cuvier, Paris, France
[3] University of Illinois at Urbana, Goodwin, Il 61801, 524 BH, 407 S, Urbana
[4] University of Otago, Department of Biochemistry, Dunedin, New Zealand

janko@iapg.cas.cz

Circum-antarctic shelf waters harbour a rare example of a marine species flock – the tribe Trematominae. This group likely originated from a benthic ancestor and contains 12 recognised species with different life histories ranging from fully benthic to cryopelagic feeders. It is unclear how they survived Pleistocene advances of continental glaciers as far as the shelf break resulting in a probable loss of habitat for benthic organisms. Pelagic ecosystems, on the other hand, might have flourished during glacial maxima due to the northward expansion of Antarctic polar waters. In order to better understand the role of ecological traits in responses to Quaternary climatic fluctuations, we performed multilocus demographic analyses of populations of four fish species, including fully benthic species as well as a cryo- and semipelagic. We revealed recent population expansion in both benthic species correlating with the last deglaciation of the Antarctic shelf, whereas the population structure of pelagic feeders either did not deviate from constant-size model or underwent much more ancient onset of major population expansion. In general, such a pattern was apparent even when comparing previously published data on other Southern Ocean organisms. Our data suggest that Pleistocene ice-sheet expansions significantly reduced the suitable habitat for benthic species, whereas different and less disruptive processes affected pelagic feeders.

05-38 Poster

THE EVOLUTION OF SPAWNING MIGRATIONS: THE ROLE OF INDIVIDUAL STATE AND POPULATION STRUCTURE

Christian Jørgensen [1], Anders F. Opdal [1], Erin Dunlop [2], Øyvind Fiksen [1]

[1] *University of Bergen, Department of Biology, PO Box 7800, N-5020, Bergen, Norway*
[2] *Institute of Marine Research, PO Box 1870 Nordnes, N-5817, Bergen, Norway*

christian.jorgensen@bio.uib.no

We use a state-dependent energy-allocation model that finds optimal life histories in different environments to study the evolution of spawning migrations in fish. It is energetically more efficient for a large fish to move, and migration distance might therefore depend on individual states such as age, size, and condition. Our study species is Atlantic cod, where some populations move few kilometres over a lifetime, while the Northeast Arctic stock historically migrated >4000 km round trip annually.

We assumed a linear relationship between migration distance and the fitness that a cod egg will have when spawned. Fitness is understood as the prospects for future survival and development that a fertilized egg faces when spawned at a particular location. We also investigated two types of behaviour: roaming migrations, where cod are free to choose their spawning site every year independently, and lifetime homing migrations, where cod choose the optimal spawning site at maturation and return every year thereafter. For both behaviours, some regions along the coast have locally high spawning biomass, and cod in good condition and of late maturation migrate farthest. The roaming behaviour, where cod choose spawning location each year depending on their individual state, leads to more population structuring along the coast, with older, larger, and fish in better condition performing longer migrations.

For both types of behaviour, life histories adapted to the current fishing regime have much shorter spawning migrations and spread over a smaller geographical range then the historical life histories. This may have consequences for the population's ability to buffer environmental variation and may lead to more variable population dynamics.

05-39 Poster

INTERPOPULATION HYBRIDIZATION AND DEVELOPMENTAL STABILITY IN DROSOPHILA SUBOBSCURA

Zorana Kurbalija [1], Marina Stamenkovic - Radak [2], Marko Andjelkovic [2]

[1] *Institute for Biological Research, Bulevar despota Stefana 142, 11000, Belgrade, Serbia*
[2] *Faculty of Biology, 11000, Belgrade, Serbia*

zorana.kurbalija@yahoo.com

Genetic coadaptation and heterozygosity are assumed to be the mechanisms that affect developmental homeostasis. The range of genetic variability affected by stress is still unknown and effects of interspecific hybridization are rather unexplored in relation to developmental stability. Along these lines, the focus of conservation biology is moving toward a population-genetic aspect of stress.

The interpopulation and intrapopulation crosses between three distinct natural populations of *Drosophila subobscura* are made in the present study. The effect of such a genomic stress is analyzed through the variability of fluctuating asymmetry (FA), a discrepancy from bilateral symmetry of wing size parameters and sternopleural bristle number in parental populations and their laboratory reared progeny. Further analysis of second generation and inversion polymorphism change would give insigth into coadaptation and/or heterozygosity as possible meschanisms which maintain developmental homeostasis in populations.

05-40 Poster

THE EFFECT OF WOLBACHIA INFECTION ON LIFE HISTORY TRAITS AND POPULATION DYNAMICS IN A MOTH

Zenobia Lewis [1], Fleur E. Champion de Crespigny [1], Stephen M. Sait [2], Tom Tregenza [1], Nina Wedell [1]

[1] *University of Exeter, Cornwall Campus, Centre for Ecology and Conservation, Tremough Campus, TR10 9EZ, Penryn, Cornwall, UK*
[2] *University of Leeds, Institute of Integrative and Comparative Biology, Tremough Campus, TR10 9EZ, Leeds, UK*

Z.lewis@exeter.ac.uk

The intracellular parasite, *Wolbachia pipientis,* is potentially the most common parasite on Earth. *Wolbachia* is transmitted almost exclusively from mother to daughter, and exhibits a number of strategies that promote the production of infected females, usually at detriment to the host. Given its widespread occurrence and its intimate association with host reproduction, *Wolbachia* may have important demographic consequences for its host. We examined the effect of *Wolbachia* infection on individual life history traits, sexual selection and population dynamics in the Mediterranean flour moth. In this species, *Wolbachia* generates cytoplasmic incompatibility (CI), which causes embryonic death when sperm from an infected male fertilises eggs from an uninfected female. We demonstrate that infected males suffer a reproductive cost in terms of reduced sperm production. Coupled with the negative effects of CI on hatching success, this means that females should avoid mating with infected males. We therefore examine whether sexual selection can ameliorate the negative impact of infection, with females avoiding copulation with infected mates, or mating multiply in order to promote sperm competition and reduce the risk of CI. At the population level, the probability of encounters between individuals of different infection status will be determined by the population structure of the host. This may limit mating opportunities and could effect the extent to which sexual selection can operate. We examine how the effects of *Wolbachia* infection on individual life history traits and sexual selection, interact with host population dynamics.

05-41 Poster

LOST IN A SELECTIVE MOSAIC? EFFECTS OF POPULATION GENETIC STRUCTURE AND GENE FLOW ON MARINE HOST-HERBIVORE INTERACTIONS IN THE BALTIC SEA

Meri Lindqvist [1], Outi Vesakoski [1], Fiia Haavisto [1], Craig Primmer [1], Veijo Jormalainen [1]

[1] *University of Turku, Biology, 20014 Turku, 20014, Turku, Finland*

meri.lindqvist@utu.fi

The littoral habitats are naturally fragmented and environmentally very heterogeneous along the Finnish coast in the Northern Baltic Sea. As a result, a geographic mosaic of selection is formed, in which ecological divergence among populations and local adaptations can be expected to arise. For the marine mesoherbivore *Idotea baltica* (Crustacea; Isopoda) these selective agents include variation both in available host species and in host quality (as food or refuge) among localities. Thus, the host – herbivore interactions are not fixed within species but are rather expected to vary among habitat types or populations. Although the littoral habitats are often geographically isolated, some dispersal is assumed to be going on among populations of *I. baltica*. The resulting gene flow connects local populations and aids the spreading of novel adaptive traits but can also erode population specific adaptations. If gene flow is occurring mostly within a habitat then this should promote local genetic differentiation between habitats. The population within the habitat could then be viewed as an evolutionary independent unit that has the potential to adapt to its local environment. Gene flow can maintain complex mosaic of interactions between hosts and herbivores by shuffling matching and mismatching traits among populations. We studied the genetic structure and gene flow among populations of *I. baltica* in the N Baltic Sea by AFLP analysis and combined this information to existing data on 1) local adaptations in host use ability and 2) differences in color morph frequencies among populations. Results indicate the existence of genetic structure between populations in the N Baltic Sea.

05-42 Poster

ADAPTATION TO NOVEL HOST PLANTS IN A HERBIVOROUS MITE: THE ROLE OF GENETIC VARIATION AND PHENOTYPIC PLASTICITY

Sara Magalhaes [1], Julien Fayard [2], Elodie Blanchet [2], Arne Janssen [3], Martijn Egas [3], Isabelle Olivieri [2]

[1] *Instituto Gulbenkian de Ciência, Evolutionary Genetics, Rua da Quinta Grande, 6, 2780-156, Oeiras, Portugal*
[2] *Unversite de Montpellier, Genetique et Environnement, 22 Place Eugene Bataillon, 34095, Montpellier, France*
[3] *University of Amsterdam, IBED, Kruislaan 320, 1098 SM, Amsterdam, The Netherlands*

smagalhaes@igc.gulbenkian.pt

When populations adapt to novel environments, individual life-history and behavioural traits are expected to be modified by changes in either gene frequencies or in phenotypic plasticity. In addition, adaptation may entail a correlated response in other environments. We studied host plant adaptation in the two-spotted spider mite, *Tetranychus urticae*. Using a base population adapted to cucumber, we established experimental populations evolving on tomato and pepper. First, we tested how long-term evolution on the ancestral host affects adaptation to two novel hosts. Using a half-sib design, we investigated whether trait changes after 15 generations of selection were related to genetic variation in the base population. Patterns of evolutionary changes generally matched those of genetic variation, and long-term evolution in a constant environment did not preclude adaptation to novel environments. We did not detect a trade-off between adaptation to the two novel hosts after 15 and after 25 generations of selection; instead, a positive correlation was found. Subsequently, we assessed whether the detection of adaptation and of the correlated response on the alternative host plant were contingent on the environment experienced by organisms. For that, mites were either sampled directly from the populations, or they had a common juvenile or maternal environment. Although the environment experienced by mites strongly affected their life-history traits, the interaction between performance and the selection regime was only significant for fecundity. Hence, detection of adaptation occurred despite strong phenotypic plasticity. We conclude that adaptation occurred through genetic changes and that it did not entail a cost in these populations, suggesting a lack of constraints on the host range of these mites, at least within the time frame considered.

05-43 Poster

THE EFFECTS OF SOCIAL ENVIRONMENT ON JUVENILE SURVIVAL IN THE GREAT TIT (PARUS MAJOR)

Stephanie P. M. Michler [1], Marion Nicolaus [1], Christiaan Both [1], Richard Ubels [1], Jan Komdeur [1], Joost Tinbergen [1]

[1] *University of Groningen, Animal Ecology Group, P.O. Box 14, 9750, Haren, The Netherlands*

s.p.m.michler@rug.nl

In each breeding attempt individuals face the decision how many male and female offspring they should produce in order to maximize their fitness. However, to assess whether skewed sex ratios are adaptive, fitness consequences of biased sex ratios need to be examined. A possible mechanism by which sex ratio adjustments on a local scale could affect parental fitness is by altering the degree of sex-specific competition that juveniles experience after independence.

In a large scale experiment we simultaneously manipulated sex ratios and densities of great tit offspring on a local scale. Thereby, we created areas where male and female juveniles experienced different competitive regimes after fledging. Observations of colour-ringed individuals over a five month period in 2005 and 2006 allowed us to gather a data set that can be examined using mark-recapture analysis. We present results on how the composition of fledglings at the end of the breeding season affected sex specific juvenile survival.

05-44 Poster

EVOLUTION OF EXTENDED LIFE SPAN IN TROPICAL FRUIT-FEEDING BUTTERFLIES

Freerk Molleman [1]

[1] *University of California, Davis, Department of Entomology, One Shields Avenue, 95616, Davis, CA, USA*

fmolleman@ucdavis.edu

Fruit-feeding butterflies in tropical forests are among the longest lived Lepidoptera. We present mark recapture data (>30 000 marked individuals, >4000 recaptured at least once) on forty-six species of fruit-feeding butterflies in Kibale National Park in Uganda. Longevity records for species of which more than 100 individuals were recaptured ranged from 67 (*Bicyclus auricruda*) to 293 days (*Euphaedra medon*). To better understand the evolution of such extraordinary long life spans we studied seasonality, nutritional ecology, and predator avoidance strategies of several long lived species. The abundance of most species varies significantly throughout the year, but seasonality was rare, and most are reproductively active in both wet and dry seasons. Fruits can be enriched in protein and amino-acids compared to flower nectar. An experiment showed that these nutrients in fruits can enable butterflies to lay eggs over a longer period of time and improve hatchability of the eggs. Therefore, use of amino acids derived from the adult diet can be partly responsible for the evolution of extended life span among fruit-feeding butterflies. Longevity was also associated with robust bodies and high escape speeds, while crypsis and aposmatism can also play a role in predator avoidance.

05-45 Poster

PECIATION OF LARGE AFRICAN BARBS IN LAKE TANA, ETHIOPIA – MTDNA GENEALOGY APPROACH.

Nikolai Mugue [1], Mikhail V. Mina [1]

[1] *Koltzov Institute of Developmental Biology, 26 Vavilov St., 119991, Moscow, Russia*

mugue@mail.ru

Lake Tana (Ethiopia) can not be considered as an „ancient lake", however it posses a spectacular and very diverse fish fauna, consisted of 12-15 morphs or species of large African barbs, belonged to *Barbus intermedius* species flock. Different forms of *Barbus* have very diverse trophic specialization, and some morphs feeds preferably on either plants, mollusks, insects, or small fishes. Therefore shape of head, eye size, pharyngeal tooth armament and length of intestine is considerably different among the morphs. Previous study on mtDNA variation demonstrated that different morphs do not form species-specific clades, but rather produce a large monophyletic cluster for all lake Tana barbs.

To reveal the degree of genetic segregation among *Barbus* morphs in lake Tana, we sequenced partial D-loop and complete CytB genes (total 1800 b.p.) in 205 specimens of three morphs: most common ancestor-like form *Barbus intermedius*, and two highly specialized morphs – *Barbus acutirostris* ("acute" or "long-snout") and *B. macrocephalus* ("big-eye"). As an outgroup, we used specimens of *Barbus intermedius* from six different rivers of Blue Nile and Genale river basins.

MtDNA genealogy approach revealed that *Barbus intermedius* consisted of highly polymorphic clade, most of specimens posses an unique mtDNA haplotypes, which corresponds with large population size and long coalescence time for this ancestral form. On the contrary, *B. acutirostris* presented by few haplotypes, and many specimens share the same haplotypes. Similar, diverse haplotype network was observed in the "Big-eye" morph. This data indicate that specialized morphs in lake Tana are reproductively isolated from the ancestral form. Different scenarios of this spectacular species flock formation are discussed.

05-46 Poster

THE EVOLUTION OF MALE CONTEST COMPETITION IN POLLINATING FIG WASPS: INFLUENCES OF SEX RATIOS, DISPERSAL AND INTERMEDIATE INBREEDING

Ronald M. Nelson [1], Jaco M. Greeff [1]

[1] *University of Pretoria, Dept. Genetics, Pretoria, South Africa*

s9816187@tuks.co.za

In mating systems we find that mate competition and population growth is influenced by the sex ratio. Pollinator fig wasps are famous for their female biased sex ratios and closed mating systems. In one species we find that intermediate inbreeding confer higher fitness and to attain this inbreeding level in the population male dispersal have developed. We argue that this may be the case for several genera as a stable polymorphism for in- and outbreeding are found by simulation modelling of haplodiploids. When dispersal occurs there is a reduction in local mate competition. In such populations, individuals with a less female biased sex ratio will be selected for. We found that there is a strong correlation between the sex ratio and male dispersal. Another effect of less female biased sex ratios is the evolution of male contest competition. With an equal sex ratio and males able to mate multiple times, females are always a limited resource and male fighting can occur. We show that the sex ratio is the main driving force for the evolution of male contest competition in pollinating fig wasps.

05-47 Poster

GENETIC DIVERSITY AND HOST SPECIALIZATION IN INVASIVE POPULATIONS OF THE PEA APHID IN CHILE

Jean Peccoud [1], Christian Figueroa [2], Andrea Silva [2], Claudio Ramirez [3], Lucie Mieuzet [1], Manuel Plantegenest [1], Jean-Christophe Simon [1]

[1] *INRA, UMR Biologie des Organismes et des Populations appliquée à la Protection des Plantes, Domaine de la Motte BP 35327, 35653, Le Rheu Cedex, France*
[2] *Universidad Austral de Chile, Instituto de Ecologia y Evolucion, Casilla 567, Valdivia, Chile*
[3] *Universidad de Talca, Instituto de Biologia Vegetal y Biotecnologia, Casilla 747, Talca, Chile*

jean.peccoud@rennes.inra.fr

The pea aphid, *Acyrthosiphon pisum*, is a pest exhibiting sympatric host-specialized populations on several species of legumes. These host-races, reported on different continents, are considered as intermediate steps in the process of sympatric speciation. *A. pisum* shows a variety of reproductive modes, from lineages alternating parthenogenesis with a yearly sexual generation (producing frost resistant eggs) to obligate parthenogenesis (favoured in regions with mild winters). We investigated the reproductive mode and the level of host specialization in populations of the pea aphid, a recently introduced species in Chile. Populations were sampled on five sympatric crops (pea, alfalfa, broad bean, lentil and red clover) in two distant sites and genotyped at 7 microsatellites loci. They appeared to be represented by four dominant clones that show striking associations with their host ranges. Phenotypic analysis confirmed their strong host specialization and parthenogenesis as their only reproductive mode. These results suggest that only a few asexual lineages of *A. pisum* successfully invaded the sampled region and became dominant on their respective hosts. When considering their relatedness to European populations feeding on the same crops, the hypothesis of multiple introductions of already specialized lineages from Eurasia to America is favoured.

05-48 Poster

DYNAMICS OF ADAPTATION IN ESCHERICHIA COLI AND THE IMPACT OF CLONAL INTERFERENCE

Lilia Perfeito [1], Lisete Fernandes [2, 3], Catarina Mota [1], Isabel Gordo [1]

[1] *Instituto Gulbenkian de Ciência, Evolutionary Biology, Rua da Quinta Grande, nº6, 2780-156, Oeiras, Portugal*
[2] *Instituto Gulbenkian de Ciência, Yeast Stress, Rua da Quinta Grande, nº6, 2780-156, Oeiras, Portugal*
[3] *Escola Superior de Tecnologia da Saúde de Lisboa, Lisboa, Portugal*

lperfeito@igc.gulbenkian.pt

All organisms have to adapt to new environments, generally by the successive accumulation of beneficial mutations. While the process of adaptation has received a great deal of theoretical investigation it is far less studied experimentally. We used a recently developed method to directly estimate the rate of appearance of beneficial mutations in *Escherichia coli* and the distribution of their effects. To complement these results we also use data from classical competition assays and computer simulations. We find that the interference caused by the competition between different lineages carrying beneficial mutations (clonal interference) has greatly underestimated previous estimates. By using a small population size we are able to measure a more accurate beneficial mutation rate, which we estimate to be on the order of 10^{-5} beneficial mutations per individual per generation. This means that about 1% of spontaneous mutations in *E. coli* are beneficial. These results can help us understand how bacteria adapt so quickly no new environments, how virulence evolves and how systems allowing recombination are maintained.

05-49 Poster

COMPARATIVE ANALYSIS OF NUCLEOTIDE POLYMORPHISM LEVELS AND SELECTION EFFICIENCY ACROSS DIFFERENT TAXONOMIC UNITS.

Natalia P. Petit [1], Antonio Barbadilla [1]

[1] *Universidad Autonoma de Barcelona, Genetica y Microbiologia, Facultad de Ciencias Edificio C, 08193, Bellaterra, Spain*

Natalia.Petit@uab.cat

The analysis of the patterns of polymorphism in different species shed light on the mechanisms of evolution of the genomes. Coding sequences of different genes and organisms have accumulated for years in Gene bank. At present, two databases (DPDB, Drosophila Polymorphism Data Base, http://dpdb.uab.es/dpdb and Mampol, Mammalia polymorphism database, http://pda.uab.es/mampol) compile sequences and estimate the levels of polymorphism for 135 species of Drosophila and 1147 species of mammals. Using this information, we designed and implemented a strategy to perform a global analysis of pattern of polymorphism among species to discover taxonomical, genomics and demographic factors affecting it. The differences in the levels of polymorphism among species and group of species were ascertained taking into account the functional category of the genes. The correlation matrix among the values of genomic features (such as genome size, percentage of repetitive DNA, CG content, codon bias, recombination rate) and synonymous polymorphism was thoroughly analyzed. The differences obtained between the Drosophila and Mammals results indicate that different selective pressures could be acting in the two species groups.

05-50 Poster

COSTS AND BENEFITS OF SOCIAL BEHAVIOURS: A RECIPROCAL TRANSPLANT OF SOCIAL SPIDERS ACROSS AN ALTITUDINAL GRADIENT

Jessica Purcell [1], Leticia Avilés [1]

[1] *University of British Columbia, Zoology Dept, 6270 University Blvd, V6T1Z4, Vancouver, BC, Canada*

purcell@zoology.ubc.ca

1. Recent studies have documented a pattern of decreasing sociality with increasing altitude both within and across social spider species in the genus *Anelosimus* in eastern Ecuador. Within this genus, subsocial species found at higher altitudes typically have small colonies containing one adult female with a single clutch, while social species found at lower elevations have larger colonies with multiple females and their offspring. We investigate what forces may be maintaining this pattern by reciprocally transplanting one subsocial and one social species between elevations.

2. Subsocial colonies transplanted to the lowlands had lower survivorship and fewer propagules relative to their native higher elevation habitat controls. We tested the hypothesis that more intense rainfall reduces survival of spiders in small subsocial colonies by sheltering nests from rain with canopies. We found that sheltered spiders survived longer and built more webbing than spiders in unsheltered nests, but all subsocial nests ultimately went extinct in the lowest transplant site. Our data suggest that predation, in particular by ants entering lowland nests, may have driven this extinction.

3. In contrast, we found no difference in survival or propagule foundation rate for social groups of the lowland social species transplanted to higher elevations when compared with their native lowland habitat controls. Additional tests indicate that the social colonies we transplanted may not have been large enough to be affected by conditions disfavouring sociality at the higher elevations.

05-51 Poster

POSSIBLE POPULATION CONSEQUENCES OF EVOLUTION OF PROSPECTING BEHAVIOUR

Irja I. Ratikainen [1], Hanna Kokko [1]

[1] *University of Helsinki, Dept of Biological and Environmental Sciences, PO Box 65, 00014, Helsinki, Finland*

irja.ratikainen@bio.ntnu.no

What is adaptive at the individual level is not necessarily beneficial for the population. This highly underexplored fact may be very relevant in relation to dispersal, since population performance may depend on individuals dispersing while individuals would often benefit from avoiding the risks of dispersal. However, even though dispersal is a very important determinant of population performance, there is still little understanding of how natural selection on this behaviour may affect population-level processes. Prospecting behaviour is an informed mode of dispersal where the individuals preferentially disperse to high quality habitat patches. We have used an individual-based simulation model to examine the consequences of evolution of this behaviour on several population traits. The selective pressures in the model are prospecting dependent mortality and varying breeding success according to habitat acquired after prospecting. For each set of parameter values we compare one scenario where the prospecting trait is set with a scenario where the trait is allowed to mutate and evolve. This comparison allows us to state whether natural selection at the individual level is good for the population. For most parameter values we found the expected results of large population sizes, a high proportion of occupied sites and high probability of population persistence in evolving compared to non-evolving populations. However, when costs of prospecting are high, i.e. high mortality while prospecting, it seems that populations would do better without natural selection. Within the examined timeframe, population sizes are higher, more sites are occupied and fewer populations go extinct in non-evolving than in evolving populations. This shows that constraints on the evolutionary process (e.g. low evolvability) can, under some circumstances, help rather than hamper population persistence.

05-52 Poster

MULTIPLE PATERNITY IN A NATURAL POPULATION OF DROSOPHILA EZOANA

Eeva Roininen [1], Jaana O. Liimatainen [1], Jouni Aspi [1], Minna Ruokonen [1]

[1] *University of Oulu, Department of Biology, POBox 3000, 90014, Oulu, Finland*

Eeva.Roininen@oulu.fi

Female remating is a common phenomenon in nature and especially studied in many insect and bird species. Remating is female's insurance against male sterility and sub-fertility and it increases genetic heterogeneity of female's offspring and therefore female's fitness. Still quite a few studies have used genetic markers to detect female remating in wild populations of *Drosophila*. In this study we examined multiple paternity in a wild *Drosophila ezoana* population in Finland. Inseminated females were collected from Oulanka National Park during the summer 2005. Remating frequency of 22 females was studied by analysing multiple paternity in their broods (from 8 to 34 daughters per mother, in total 473 flies) by using two X chromosomal and five autosomal microsatellite loci. Our results show high frequency of remating. All broods had at least two fathers and some as many as six (on average 4,1). Population structure in general and the influence of female remating to effective population size in this population is also studied.

05-53 Poster

MOLECULAR IDENTIFICATION OF THE DROSOPHILA VIRILIS GROUP SPECIES

Jarkko Routtu [1], Maaria Kankare [1]

[1] *University of Jyväskylä, Department of Bio and Environmental Science, Jyväskylä, Finland*

jarkko.routtu@bytl.jyu.fi

Drosophila virilis group flies are widely used in evolutionary research. These species share common characteristics, like large size for a *Drosophila* fly and a black spot on the longest cross vein of the wing, which make the group level identification easy. However, species within the *D. virilis* group are hard to identify, as many of them are cryptic and distributed sympatrically. Methods like mating laboratory males with wild caught females as well as identifying F1 generation male songs have been used for identification purposes. Unfortunately these methods are very time and resource consuming. We have developed an identification method which is based on different allele lengths in several microsatellite loci. From the set of 50 loci, fourteen could be amplified in all the *D. virilis* group species. These fourteen loci resulted in structured phylogeny that separates most of the species. Especially, population demography and history of global populations in *D. montana*, *D. ezoana* and *D. littoralis*, that occur sympatrically in Finland were classified by the microsatellites. Subsets of the loci can also be used for rapid identification of the previously mentioned species with Spreadex^{TM} gel electrophoresis. Evolutionary studies using wild populations of *D. virilis* group species are now more accessible for researchers with the aid of these faster identification methods.

05-54 Poster

NON-GRADUAL VARIATION IN COLOUR MORPHS OF THE STRAWBERRY POISON FROG DENDROBATES PUMILIO: GENETIC AND GEOGRAPHIC ISOLATION SUGGEST A ROLE FOR SELECTION IN MAINTAINING POLYMORPHISM

Andreas Rudh [1], Björn Rogell [2], Jacob Höglund [2]

[1] *Uppsala University, Animal Ecology, Norbyv. 18 D, SE-752 36, Uppsala, Sweden*
[2] *Uppsala University, Population Biology and Conservation Biology, Norbyv. 18 D, SE-752 36, Uppsala, Sweden*

andreas.rudh@ebc.uu.se

The relative role of geographic isolation and selection in driving population divergence remains one of the central questions in evolutionary biology. We approached this question by investigating genetic and morphologic variation among populations of the strawberry poison frog *Dendrobates pumilio* in the Bocas del Toro archipelago, Panama. We found a significant population genetic structure and isolation by distance based on AFLP markers. Snout vent length (SVL), colouration and extent and size of dorsal black spots varied extensively among the studied populations. SVL and brightness of colour changed gradually with geographic distance while the black spot patterns and other colouration parameters did not show a gradual change. The latter characters could be dramatically different even between populations located nearly each other on the same island. These results imply that neutral divergence among populations may account for the genetic patterns based on AFLP markers, SVL and brightness but that some form of selection need to be invoked in explaining the extraordinary variation in spot size and coverage, saturation and hue. We discuss the possibility that the observed variation in colour morphs is a consequence of a combination of local variation in both natural selection on an aposematic signal towards visual predators and sexual selection generated by morph specific mate preferences.

05-55 Poster

THE INFLUENCE OF MATERNAL CARE IN SHAPING HUMAN SURVIVAL AND FERTILITY

Samuel Pavard [1], David N. Koons [1], Evelyne Heyer [2]

[1] *Max Planck Institute for Demographic Research, Laboratory of Survival and Longevity, Konrad Zuse Strasse, 1, 18057, Rostock, Germany*
[2] *Museum National d'Histoire Naturelle, Hommen, Nature et Societe, 17 place du Trocadero, 75116, Paris, France*

pavard@demogr.mpg.de

The influence of maternal care on child survival has evolved throughout human history due to variation in altriciality, allocare and maternal behaviors. Here, we study the impact of these factors on forces of selection acting on age-specific survival and fertility. To do that, we performed elasticity analysis in a model that incorporates the dependence of child survival on maternal survival. Results reveal life-history changes that cannot be elucidated when considering child's survival independent of maternal survival: decrease of late fertility *and* increase of late survival, and concomitant decrease of early *and* late fertility. We also show that an increase of child altriciality in early humans might explain the main human life-history traits: a high life expectancy and post-reproductive life; a long juvenile period and a higher, and narrowed, fertility at the peak of the reproductive period. Our results therefore indicate that maternal care may have shaped the human life-history.

05-56 Poster

PREVALENCE AND ASSOCIATIONS OF FUNGAL ENDOPHYTES UNDER ENVIRONMENTAL STRESSES

Nora M. Saona [1], Dawn R. Bazely [1]

[1] *York University, Department of Biology, 4700 Keele Street, M3J 1P3, Toronto, Canada*

nsaona@yorku.ca

Interactions between fungal endophytes and grasses are generally considered to be mutualistic. Yet, environmental stresses may influence the nature of endophyte-grass interactions (mutualistic to antagonistic) and potentially affect endophyte prevalence in natural populations. We investigated how environmental factors affect the prevalence and nature of interactions between the fungal endophyte *Epichloë festucae* (Clavicipitaceae) and Red Fescue grass (*Festuca rubra*: Poaceae) in the Skeppsvik archipelago, Sweden. We screened grasses for endophytes with an immunoblot assay and related endophyte prevalence to soil nutrient and water availability, intensity of herbivory by geese, and island age. Soil moisture had a predominant influence on the prevalence of endophytes, and its effect varied with nutrient availability, grazing intensity and island age. Endophyte-infected individuals produced fewer inflorescences than did uninfected individuals, and endophyte prevalence decreased with population age. Although these data suggest that endophytes are interacting antagonistically with their hosts, abiotic factors appear to mediate this association. We also conducted a greenhouse experiment to determine how nutrient and water supplementation affects the endophyte-grass symbiosis. We found that endophyte-infected plants produced fewer tillers than uninfected plants, supporting conclusion that endophytes are interacting antagonistically with grasses.

05-57 Poster

'TAKE-AWAY' FORAGING SPATIALLY UNCOUPLES PREDATOR AND PREY-ATTACK DISTRIBUTIONS

Isabel M. Smallegange [1], Jaap Van der Meer [1], Maurice W. Sabelis [2]

[1] *Royal Netherlands Institute for Sea Research (NIOZ), Marine Ecology and Evolution, P.O.Box 59, 1790 AB, Den Burg (Texel), The Netherlands*
[2] *Institute for Biodiversity and Ecosystem Dynamics, Section Population Biology, P.O.Box 94084, 1090 GB, Amsterdam, The Netherlands*

smallegange@orn.mpg.de

Ideal-free distribution (IFD) theory is an important game-theoretical tool in understanding why animals forage where they forage. IFD theory assumes foragers in a patchy environment to maximize fitness and hence their feeding rate by balancing gains from more food against losses from more competition. Ultimately, individuals cannot increase their feeding rate by moving to another patch and they distribute over patches in proportion to prey density per patch. However, the implicit assumption that catch should match time spent in a prey patch is not met in our experiments with shore crabs (*Carcinus maenas*) foraging on two adjacent patches with mussels (*Mytilus edulis*). Despite aggregating their attack where it is most profitable shore crabs distributed themselves homogeneously across mussel patches: they 'take away' the prey caught and consume it elsewhere to reduce interference. Thus, predator distribution can be quite different from prey-attack distribution. This is important because the latter is shown to be decisive for persistence of predator and prey populations in ecological models.

05-58 Poster

FITNESS CONSEQUENCES OF THE TRANSITION TO OBLIGATE ASEXUALITY IN A CYCLICAL PARTHENOGEN

Claus-Peter P. Stelzer [1]

[1] *Institute for Limnology of the Austrian Academy of Sciences, Mondseestrasse 9, 5310, Mondsee, Austria*

claus-peter.stelzer@oeaw.ac.at

Although the majority of all eukaryotes reproduce sexually, obligate asexual lines have been found in numerous animal and plant groups. Transitions to obligate asexuality have been reported frequently in cyclical parthenogenes, animals whose life cycles contain both sexual and asexual stages. For instance, in monogonont rotifers some clones have permanently lost all sexual parts of their life cycle. Such newly formed obligate asexual lines provide a test case for examining the fitness consequences of obligate asex in organisms with complex life cycles.

In this study, I used laboratory experiments to estimate fitness in obligately asexual vs. cyclically parthenogenetic lines of the rotifer *Brachionus calyciflorus*. Several clones were investigated - clones that have undergone a recent transition to asexuality (< 50 generations ago) and closely related clones that produced a high proportion of sexual daughters. Fitness was measured in several different ways and on the individual and population level (individual reproduction, population growth rate, carrying capacity). The results indicate that obligate asexuals, in addition to having faster population growth during population expansion, can also exhibit a higher carrying capacity and tolerate lower ambient resource levels during phases of population stagnation. These latter features suggest that asexual populations can be well buffered against invading sexuals, by means of a modification of their environment.

05-59 Poster

HOW SYNERGY PROMOTES CO-OPERATION

David Sumpter [1]

[1] *University of Oxford, Zoology, Oxford, UK*

david.sumpter@zoology.oxford.ac.uk

An enduring question in evolutionary biology concerns the mass co-operation of unrelated animals in situations where individuals have the possibility to cheat. The chemical trails of rats and ants, cliff sparrow food calling, bark beetles joint attack on trees, all involve the use of costly signals that improve group efficiency. A striking aspect of many such co-operative behaviours is that in a population of individuals where no-one engages in co-operative signalling it does not pay any one individual to start co-operating. How then does co-operation evolve? I discuss a unifying answer to such problems. I use an n-player game theoretic model to show that co-operation can evolve in such settings provided that 'productivity' of the group is more than the sum of its parts and this productivity is divided equally between group members. I argue that such synergistic interactions are widespread in Nature, with non-linear interactions of group members producing collective patterns that are more than the sum of their parts (Sumpter 2006). This approach clarifies a number of misunderstandings where individuals in such groups have been classified as being 'altruistic' despite the absence of kin selected benefits. By determining the mechanisms through which co-operation is manifested, and in particular by studying how functional collective patterns can self-organise from simple interactions between individuals, we can better understand how it evolved through natural selection.

Sumpter, D. J. T. 2006 The principles of collective animal behaviour. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **361**, 5-22.

05-60 Poster

THE EVOLUTION OF PREDATORY BEHAVIOUR AND ITS EFFECT ON THE DYNAMICS OF A TRI-TROPHIC SYSTEM

Beata Sznajder [1], Martijn Egas [1], Maurice W. Sabelis [1]

[1] *University of Amsterdam, Population Biology, Kruislaan 320, 1098 SM, Amsterdam, Netherlands*

sznajder@science.uva.nl

We study an ecological community consisting of three trophic levels: predators, their herbivorous prey and the plants. Our focal species, *Phytoseiulus persimilis,* is the predator of the spider mite *Tetranychus urticae,* which feeds on a wide range of plant species. Substantial evidence shows that plants attacked by herbivores, including *T. urticae*, release a species-specific blend of volatile compounds. More importantly, this blend is also specific for the species of the attacker. As such, these volatiles may serve as a signal of herbivore- presence and were postulated to be effectively used by natural enemies. Indeed, empirical studies showed that many predatory species, including *P. persimilis* are attracted to the volatiles of infested plants. Together this indicates a potential for evolutionary dynamics characterized by honest or dishonest signalling on the part of the plants and evolutionary responses on the part of the evading prey and foraging predators.

We studied foraging behaviour of *P. persimilis* originating from natural populations in Sicily. In particular, we examined whether there is genetic variation in the predatory responses to the plant-derived volatiles, and what behavioural types are most prevalent among the predators. Our results show the presence of genetic variation and a substantial variety in behavioural responses to plant signals of varying complexity. Based on our results we discuss how the patterns of behaviour may affect the evolution of predatory responses and how this will translate into the structure and functioning of the community of plants and herbivores.

05-61 Poster

GROWTH RATES AND REPRODUCTIVE EFFORT OF MALE MOOSE (ALCES ALCES): THE EFFECTS OF HARVEST-INDUCED EXTRINSIC MORTALITY

Raisa T. Tiilikainen [1], Tuire Nygrén [2], Vesa Ruusila [1]

[1] *Finnish Game and Fisheries Research Institute, Joensuu Game and Fisheries Research, Yliopistokatu 6, 80100, Joensuu, Finland*
[2] *Finnish Game and Fisheries Research Institute, Ilomantsi Game Research Station, Haravapurontie 4, 82900, Ilomantsi, Finland*

raisa.tiilikainen@rktl.fi

Age and size at maturation are important life-history traits influencing survival, reproductive effort and growth, and among the most important life history trade-offs are trade-offs between current and future reproduction and survival. These are predicted to evolve in response to differences in extrinsic mortality rates: Increased mortality of immature individuals should result in earlier onset of maturation. When survival and hence future reproductive success is decreased due to increased extrinsic mortality, should the investment in current reproduction increase because of lower costs to survival and future reproduction. We used harvest data about age, body weight, antler spread and tine number of intensively harvested moose Alces alces in Finland, and compared the growth rates of weight and antlers after i) adult-biased, and ii) both adults and calves targeted harvesting. To study the male current reproductive effort we combined the two antler measures and proportioned it to the body weight. After mixed age class hunting growth rates of both body weight and antlers of young males were significantly higher compared to the period of adult-biased hunting structure. Also, the increased extrinsic mortality induced higher reproductive effort at younger ages. Younger males invested less to antler growth relative to body weight than prime-aged males, but as the mortality rates increased, the young invested more to antler growth, and thus to reproduction. Our results suggest that increased extrinsic mortality induces higher growth rates of body weight and antler size, and higher reproductive investment at younger ages in male moose.

05-62 Poster

THE EVOLUTION OF ‘INTELLIGENT’ DISPERSAL STRATEGIES DRIVES THE SPATIAL DYNAMICS OF POPULATIONS WITH STATIONARY AND EXPANDING RANGES.

Justin M. J. Travis [1]

[1] *University of Aberdeen, School of Biological Sciences, Zoology Building, Tillydrone Avenue, ab242tz, Aberdeen, UK*

justin.travis@abdn.ac.uk

Here, I will describe the results of recent work that has extended previous theory on dispersal evolution in two important directions. First, I will describe an individual-based coupled map lattice model in which a three parameter density-dependent dispersal strategy is allowed to evolve. The model is similar to one published recently by Kun & Scheuring (2006), but with the important difference that we do not follow the standard adaptive dynamics method of sequentially tracking the success of a single mutant in competition with the resident. Instead we have a rate of mutation, and there can be many different phenotypes in the population at any one time. Using this model we show that selection pressure on dispersal strategy during range expansion is very different to that in a stationary population, and that dispersal evolution can lead to rapidly accelerating rates of spread. We also demonstrate that the acceleration of range expansion is much greater when a density-dependent strategy evolves than when a density-independent strategy is modelled. Secondly, I describe work that models the evolution of inter-patch movement behaviour using biased correlated random walks. Results demonstrate that the evolved pattern of movement depends critically upon the cost of dispersal but also varies according to the reproductive rate and the distance between patches. Mal-adaptation in dispersal strategy can have important consequences for the spatial population dynamics. I argue that future studies on the evolution of dispersal are required, and that they should focus on increasing the realism of dispersal behaviour, consider more than simply emigration rates, and start to explicitly incorporate the genetics underlying dispersal-relevant traits.

Kun, A. & Scheuring, I. 2006. The evolution of density-dependent dispersal in a noisy spatial model. *Oikos* **115**: 308-320.

05-63 Poster

CLIMATE-DRIVEN MATERNAL EFFECTS ON OFFSPRING SEX RATIO IN A VIVIPAROUS LIZARD

Erik Wapstra [1], Tobias Uller [2], Mats Olsson [2], David Sinn [1], Rick Shine [3]

[1] *University of Tasmania, Australia*
[2] *University of Wollongong, Australia*
[3] *University of Sydney, Australia*

uller@uow.edu.au

Maternal effects are increasingly acknowledged as important factors in adaptive evolution, in particular under fluctuating environmental conditions. Here we show that populations of the viviparous snow skink, *Niveoscincus ocellatus*, at the climatic extremes of the species’ distribution differ in the degree to which maternal thermal conditions affect offspring sex ratio at parturition. In skinks from lowland populations, relatively high thermal (basking) opportunity results in excess of females and *vice versa* whereas, in an alpine population, maternal thermal opportunity does not affect offspring sex ratio. As a consequence, offspring sex ratio fluctuates significantly among years in the lowland population and is strongly correlated with annual thermal conditions experienced in the field. In the highland population, however, no annual variation in offspring sex ratio exists. The results are discussed from a perspective of sex allocation theory and the role of maternal effects as causes of phenotypic variation in relation to environmental change.

05-64 Poster

SPATIAL RELATEDNESS AND BROOD PARASITISM IN A FEMALE-PHILOPATRIC BIRD POPULATION

Peter Waldeck [1], Malte Andersson [1], Mikael Kilpi [2], Markus Öst [3]

[1] *Göteborg University, Dep of Zoology, Box 463, 405 30, Göteborg, Sweden*
[2] *Aronia Research Centre, Raseborgsvägen 9, 10600, Ekenäs, Finland*
[3] *Helsinki university, Department of Biological and Environmental Sciences, PO Box 65, 00014, Helsinki, Finland*

peter.waldeck@zool.gu.se

The spatial structure of relatedness between individuals in a population can be crucial for social selection and evolution. We analyse kinship in relation to spatial relatedness pattern and an alternative female reproductive tactic, conspecific brood parasitism (CBP), in two populations of common eider *Somateria mollissima* (Baltic Sea and Hudson Bay). In waterfowl, females tend to breed near their birth site. Relatedness between females might therefore be a contributing factor in CBP.

Spatial relatedness structure differed between the two populations. In the Baltic Sea spatial relatedness decreased with increasing nests distance, as expected from strong natal philopatry. In the Hudson Bay population we found no such trend.

Pairwise relatedness in host-parasite pairs was higher than that between close neighbours. The spatial relatedness trend in the Baltic Sea suggests that the high host-parasite relatedness may in part be explained by natal philopatry, but several aspects indicate that this is not the full explanation. High host-parasite relatedness in Hudson Bay was clearly not a consequence of natal philopatry alone.

The similar results as regards host-parasite relatedness in these two populations of eiders breeding under different environmental conditions suggest that relatedness may be an important factor in brood parasitism in eiders. Furthermore, as high host-parasite relatedness could not be explained by natal philopatry alone, some additional form of kin bias is involved. One candidate mechanism for future study is association between birth nestmates.

05-65 Poster

HYBRIDIZATION OR INCOMPLETE LINEAGE SORTING?
– A CASE STUDY OF A PAIR OF SISTER SPHAGNUM SPECIES

Ping Zhou [1], Arthur J. Shaw [1]

[1] *Duke University, Department of Biology, 27708, Durham, North Carolina, U.S.A.*

ping.zhou@duke.edu

The interpretation of shared polymorphisms between sister species is always controversial without biological information. The two competing explanations are incomplete lineage sorting and hybridization. This study is to use DNA sequences from 6 loci to infer the speciation process between two *Sphagnum* species (*S. macrophyllum* and *S. cribrosum*). Twenty-seven herbarium collection materials from 25 populations are screened for the 6 loci. The combined phylogenetic analyses showed that *S. macrophyllum* and *S. cribrosum* are reciprocally monophyletic. Genetic analyses based on the neutral coalescence model using summary statistics suggest that the simplest allopatric speciation model—isolation model with no subsequent gene flow and constant population sizes cannot be rejected. However, the data do suggest asymmetric gene flow between the two species since divergence under another speciation model-- "isolation with migration", which is implemented in Bayesian framework using Markov chain Monte Carlo method. Field works have identified 42 extra populations of these species. Moreover, we found three sympatric populations and one of them have abundant both species with sexual reproduction. The comparative study of polymorphisms from sympatric populations and allopatric populations demonstrate that there is strong reproductive isolation between *S. macrophyllum* and *S. cribrosum*. And *S. macrophyllum* becomes paraphyly when the samples from northern part of North America are included. These results suggest that incomplete lineage sorting would be a plausible explanation for the shared polymorphisms between these two species.

6

The role of natural enemies in diversification

Thursday August 23 *Location*: University building IX

Symposium 6: The role of natural enemies in diversification

ORGANIZERS: Steven Vamosi, University of Calgary, Canada
Patrik Nosil, Simon Fraser University, Canada

9.45-10.15	**James Mallet** (invited) Mullerian mimicry and speciation
10.15-10.45	**Karsten Schonrogge** (invited) Factors determining the composition of parasitoid assemblages attacking oak cynipid galls
10.45-11.05	**Erik Svensson** Selective predation on species recognition characters and wing morphology in sympatric damselflies (genus Calopteryx)
11.05-11.35	*Coffee*
11.35-11.55	**Justin Meyer** Competition, predation, and diversification
11.55-12.15	**Johanna Mappes** Changes in predator community generate seasonally varying selection for warning signals
12.15-12.35	**Andrew MacColl** Can parasites drive the adaptive radiation of host populations?
12.35-12.55	**Bryan Clarke** Experiments on the maintenance of polymorphism by bird predators
	Lunch

06-01 Talk

MULLERIAN MIMICRY AND SPECIATION

James Mallet [1]

[1] *University College London, Biology (Galton Laboratory), 4 Stephenson Way, London NW1 2HE, UK*

j.mallet@ucl.ac.uk

The tropical rainforest East of the Andes contains the greatest diversity of terrestrial organisms on the planet. Biotic interactions are intense leading to adaptations such as the mutualistic use of shared warning colour patterns (Mullerian mimicry) by multiple species of butterflies. I here explore the interaction between the evolution of mimicry and speciation. I discuss new and emerging evidence for sharing of mimicry adaptations between species via hybridization and introgression, and also via hybrid speciation, in *Heliconius* butterflies.

06-02 Talk

FACTORS DETERMINING THE COMPOSITION OF PARASITOID ASSEMBLAGES ATTACKING OAK CYNIPID GALLS

Karsten Schönrogge [1], Graham Stone [2], Richard Bailey [2], James Cook [3], George Melika [4], György Csóka [5]

[1] *NERC Centre for Ecology and Hydrology, CEH Wallingford, UK*
[2] *Edinburgh University, Institute of Evolutionary Biology, UK*
[3] *Reading University, School of Biological Sciences, UK*
[4] *Systematic Parasitoid Laboratory, Köszeg, Hungary*
[5] *Forest Protection Service, Mátrafüred, Hungary*

ksc@ceh.ac.uk

A major goal of ecology is to understand patterns in the diversity and structure of communities. Insects are particularly diverse and parasitoids and their insect hosts have coevolved to produce diverse communities that comprise about a third of all animal species. However, the factors structuring these communities remain poorly understood and most studies lack an evolutionary perspective. We studied the diverse and closed communities of parasitoids that attack oak gall wasps, hosts which display great variation in the forms of galls that they produce and where and when they develop. This way we divide host traits into female, host location traits and larval, gall morphology- or defence traits and ask which affect the composition of associated parasitoid assemblages. Knowledge of the determinants of assemblage structure should allow predicting new host-parasitoid combinations that may result from both species introductions and range expansions.

06-03 Talk

SELECTIVE PREDATION ON SPECIES RECOGNITION CHARACTERS AND WING MORPHOLOGY IN SYMPATRIC DAMSELFLIES (GENUS CALOPTERYX)

Erik I. Svensson [1], Magne Friberg [2]

[1] Section for Animal Ecology, Department of Ecology, Lund University, SE-223 62, Lund, SWEDEN
[2] Department of Zoology, Stockholm University, SE-106 91, Stockholm, SWEDEN

erik.svensson@zooekol.lu.se

Although predation is thought to affect species divergence, the effects of predator-mediated natural selection on species divergence and in non-adaptive radiations have seldom been studied in natural populations. Wing melanization in *Calopteryx*-damselflies have important functions in sexual selection, interspecific interactions as well as in species recognition. The genus *Calopteryx* and other damselfly genera have also been put forward as examples of radiations driven by sexual selection. We show that avian predation strongly affects natural selection on wing morphology and male wing melanization in two congeneric and sympatric species of this genus (*C. splendens* and *C. virgo*). Predation risk was almost three times higher for *C. virgo*, which has an exaggerated degree of wing melanization, compared to the less exaggerated, sympatric congener *C. splendens*. Selective predation on the exaggerated species *C. virgo* favored a reduction and redistribution of the wing melanin patch. There was evidence for non-linear selection on wing patch size, wing patch darkness, wing length and width in *C. splendens* but weaker non-linear selection on the same trait combinations in *C. virgo*. Selective predation could interfere with species divergence by sexual selection and may thus indirectly affect male interspecific interactions, reproductive isolation and species coexistence in this genus.

06-04 Talk

COMPETITION, PREDATION, AND DIVERSIFICATION.

Justin R. Meyer [1], Rees Kassen [1]

[1] University of Ottawa, Biology, 30 Marie Curie, K1N 6N5, Ottawa, CANADA

justin.raymond.meyer@gmail.com

Adaptive radiation is one of the most celebrated features of evolution and may be responsible for much of the diversity of life that exists today. Much attention has been given to the role of resource competition as the mechanism driving both the phenotypic divergence and rapid diversification that are the hallmarks of the process. The role of predation in adaptive radiation, however, has received little attention. For this talk I will discuss how we used experimental evolution in the bacterium *Pseudomonas fluorescens* to provide the first, direct, evolutionary test of the role of predation, and how it interacts with resource competition, to cause bacteria to diversify into novel spatial niches in a laboratory microcosm. By independently manipulating the presence and absence of resource competition and predation (by the protist *Tetrahymena thermophila*), we estimate the frequency-dependent fitness functions of evolved *Pseudomonas* in relation to its ancestor. We find that either competition or predation alone are sufficient to drive the radiation, but also, that there is no synergism between them in promoting the radiation. This is because when predation is sufficiently strong to drive diversification on its own, the resulting reduction in bacterial densities minimizes competition and slows diversification. Additionally, we found that diversification in the presence of the predator is less repeatable; suggesting that the mortality imposed by predators can cause the stochastic processes of mutation and drift to have a greater influence on diversification. Overall, our results suggest that predation may play an under-appreciated role in driving adaptive radiations.

06-05 Talk

CHANGES IN PREDATOR COMMUNITY GENERATE SEASONALLY VARYING SELECTION FOR WARNING SIGNALS

Johanna Mappes [1], Katja Ojala [1], Hanna Kokko [2], Leena Lindström [1]

[1] *University of Jyväskylä, Department of Biological and Environmental Science, Survontie 9, 40014, Jyväskylä, Finland*
[2] *University of Helsinki, Department of Biological and Environmental Science, P.O. Box 65, 00014, Helsinki, Finland*

mappes@bytl.jyu.fi

Antipredatory defence strategies show enormous diversity, a prime example being variation in animal colour patterns. However, temporally varying selection, a generally potent force maintaining variation in strategies, has been overlooked in the context of aposematic signals, i.e. warning colours that communicate to potential predators that the bearer of the signal is unprofitable, and thus reduces the likelihood of being preyed upon. We show that the benefits of aposematism as an anti-predatory strategy change seasonally according to the age structure (and thus experience level) of the predator community. Conspicuous warningly coloured prey suffer higher mortality than more inconspicuous prey when naïve predators (fledglings) are common, while the reverse is true before and after the fledgling period. We also show that the prevalence of warningly coloured Finnish macrolepidopteran larvae is lower in the main fledgling period. Our results show that the problem of individuals 'altruistically' educating predators (since they themselves die doing so) applies to the maintenance phase and not only to the origin of aposematism, and can explain the relative rarity of aposematic strategy.

06-06 Talk

CAN PARASITES DRIVE THE ADAPTIVE RADIATION OF HOST POPULATIONS?

Andrew D. C. MacColl [1]

[1] *University of Nottingham, School of Biology, University Park, NG7 2RD, Nottingham, UK*

andrew.maccoll@nottingham.ac.uk

The ecological theory of adaptive radiation states that phenotypic divergence and speciation occur when a lineage invades, and then adapts to, a novel array of selective environments. Parasites are a major component of the selective environment of most organisms and, as novel environments will typically contain new parasites, we should expect that host-parasite interactions will contribute to local adaptation and species formation. However the possibility that spatial variation in parasitism could cause host populations to diverge has hardly been considered. Three-spined stickleback (*Gasterosteus aculeatus* complex) have undergone a classic adaptive radiation since their invasion of freshwater from the sea. In this talk I will examine whether parasites are an important source of divergent selection between environments and whether host species become locally adapted to parasites in different environments. I will use observational and experimental data to address three questions: (1) Does invasion lead to a change in parasitism? (2) Does change in parasitism lead to divergence? (3) Could divergence contribute to speciation? In so doing I will show that there is good evidence that parasitism can contribute to the adaptive radiation of host populations.

06-07 Talk

EXPERIMENTS ON THE MAINTENANCE OF POLYMORPHISM BY BIRD PREDATORS

Bryan C. Clarke [1], Oliver Craig [2], Clare Green [3], Peter Shelton [4]

[1] University of Nottingham, Institute of Genetics, Queens Medical Centre, NG72UH, Nottingham, United Kingdom
[2] Universita di Roma "Tor Vergata", Dipartimento di Biologia, Via della Ricerca Scientifica 1, 00133, Roma, Italy
[3] 15 Kirby Close, Wootton, NN46AB, Northampton, United Kingdom
[4] Maptek, Suite 1, 50 Berry Street, NSW2060, North Sydney, Australia

bryan.clarke@nottingham.ac.uk

Many prey species have striking colour polymorphisms that seem to be unconnected with mimicry. Earlier experiments have shown that, when the prey are not too dense, predators tend disproportionately to over-eat common morphs of the prey, and to ignore rare ones. We describe experiments that examine the behaviour of wild birds hunting for artificial polymorphic caterpillars. They show how the predators can maintain polymorphisms not only in the colours but also in the shapes of their prey (albeit less easily). They suggest that the predators do not form a 'gestalt' image, but treat colour and shape independently. They also show how predation can bring about divergence between sympatric, or even allopatric, populations.

06-01 Poster

SHORE CRABS, SNAILS, AND 'SERIAL SPECIATION'.

John W. Grahame [1], Geoffrey C. Trussell [2]

[1] University of Leeds, Institute of Integrative & Comparative Biology, LC Miall Building, Clarendon Way, LS2 9JT, Leeds, UK
[2] Northeastern University, Marine Science Center, 430 Nahant Road, Nahant, MA 01908, Boston, USA

j.w.grahame@leeds.ac.uk

Parallel speciation is the recurrence of speciation events in different places, driven by the same ecological processes in each instance. But if ecology is important in speciation, might we not look for evidence on the temporal axis, as well as the spatial? For serial speciation, as well as parallel?

The intertidal is a very strong environmental gradient. In northern Europe the most derived species of the clade *Littorina* (*L. saxatilis*) shows contemporary divergence which seems to be at least partly driven by the low-shore crab *Carcinus maenas*. Divergent morphs of the snail are crab-avoiders and crab-resisters. On the east coast of North America less strong differentiation is evident, this would be consistent with the more recent exposure of the snail to the crab. These divergences are consistent with the parallel speciation model. In Spain, there is another divergence in the same prey species, this time responding to predation from the high-shore *Pachygrapsus marmoratus*. This divergence presents similar morphological adaptations in the prey species as does that in northern Europe (and North America) but is ‘upside down’, following the predator.

In two less derived sister species pairs, shell morphology again indicates crab-avoiders and crab-resisters. We suggest that crab predation was important in these diversifications as well: these older speciations show the signature of response to a shell-breaking predator, just as the modern diversificiation in *L. saxatilis* does.

Finally we ask whether the North Atlantic littorinids represent a peculiar system, or whether other clades show similar features.

06-02 Poster

BACTERIA-PHAGE COEVOLUTION AS A CAUSE OF BACTERIAL DIVERSITY

Ivana Gudelj [1], Sinan S. Arkin [2], Robert E. Beardmore [2]

[1] *University of Bath, Department of Mathematical Sciences, Claverton Down, BA2 7AY, Bath, UK*
[2] *Imperial College London, Department of Mathematics, South Kensington Campus, SW7 2AZ, London, UK*

i.gudelj@maths.bath.ac.uk

Understanding mechanisms that facilitate creation and maintenance of bacterial diversity is an important challenge facing a range of scientific disciplines including epidemiology and evolutionary ecology. Pathogens such as bacteriophage are implicated increasingly frequently in the processes that create and maintain bacterial diversity but it has become apparent that bacteria and phage do not evolve in isolation. Instead phage impose selection for resistant bacteria which in turn impose selection for infective phage, resulting in antagonistic co-evolution.

In this theoretical study we develop a model of bacteria-phage co-evolution in the chemostat where the infection process is modelled as an imperfect lock-and-key mechanism whereby every phage tail fiber could adsorb to multiple bacterial surface receptors but with different efficiencies. We consider how microbial species co-evolve under conditions in which mutations of both small and large phenotypic effect can enter populations at any time and the fitness of mutants depends on the environment in which they occur, forming a feedback loop between ecological and evolutionary processes. Our model generates a series of predictions that can be tested experimentally: bacterial density decreases and phage density increases as the chemostat dilution rate decreases; presence of phage dramatically increases bacterial diversity; in the presence of phage bacterial diversity peaks at intermediate resource concentrations.

06-03 Poster

VARIATION IN THE COLORATION OF ISOPOD IDOTEA BALTICA IN DIFFERENT PLANT COMMUNITIES: PREDATION CAUSING LOCAL ADAPTATIONS

Fiia Haavisto [1], Outi Vesakoski [1], Veijo Jormalainen [1]

[1] *University of Turku, Department of Biology, 20014, Turku, Finland*

fiia.haavisto@utu.fi

Environmental heterogeneity causes selection to vary within the distribution of a species. Owing to this variation, adaptations seen in populations may not be consistent through the species' distribution range but depend on the nature of environment. Studies concerning adaptations of herbivores have mainly concentrated on traits evolving in plant–herbivore interactions. Local adaptation can however arise through the action of the third trophic level when selection acts on traits important in survival such as animal coloration. Here we studied variation in the herbivore coloration between different plant communities and the role of predation as a selective agent. We collected population samples of the color polymorphic herbivorous isopod *Idotea baltica* from four sea grass (*Zostera marina*) meadows and from four bladder wrack (*Fucus vesiculosus*) belts, and determined their color morph frequencies. Moreover, we studied whether morph frequencies were permanent by comparing adult and juvenile frequencies sampled from the same population first in the spring and then in the autumn. Differences in isopod color morph frequencies between distinct plant communities, temporal consistency and reoccurrence of these differences in geographically separated but vegetationally similar areas indicate that isopods are adapted by their coloration to local environment. We further studied whether selective predation by perch (*Perca fluviatilis*) could cause variation in survival of colour morphs in different plant communities. We found that predation indeed is an important selective agent acting on isopod coloration since the risk of morphs getting caught by a fish predator depended on the coloration of an individual. Instead, predation pressure on different colour morphs was similar in the two plant communities.

06-04 Poster

MORPHOLOGICAL DIMORPHISM CAUSED BY FUNCTIONAL TRADE-OFF IN RESOURCE HANDLING STRATEGIES

Junji Konuma [1], Satoshi Chiba [1]

[1] *Tohoku University, Graduate School of Life Sciences, Aobayama, 980-8578, Sendai, Japan*

konuma@mail.tains.tohoku.ac.jp

We explored how functional trade-offs in resource handling strategies are associated with the divergent morphology of predators. The malacophagous carabid, *Damaster blaptoides*, shows two extreme morphologies in the forebody: there is an elongate small-headed type and a stout large-headed type. Large-headed beetles can readily crush snail shells with their powerful jaws, but cannot insert their oversized heads into the shells. In contrast, small-headed beetles can insert their heads into the shells for direct predation on snail bodies, but poorly crush the shells because of their frugal jaws. Thus, crushing and inserting are alternatively effective in feeding on snails. Carabid beetles that feed on snails tend to have an extremely slender or stout forebody compared with beetles that eat insects and earthworms. Phylogenetic studies show that adaptations for snail feeding led to the diversification of beetle heads. Interestingly, it has been demonstrated that the same trade-off diversifies shell morphology in studies of freshwater snails, where elongate shells are adaptive in protecting against entry attacks and rounded shells are adaptive in protecting against crushing attacks. The functional trade-offs in snail handling strategies have a significant, important role in both morphologies of snails and snail predators in evolution.

06-05 Poster

INCREASED PREDATION RISK AS A COST OF INCREASED GROWTH RATE ALONG A LATITUDINAL GRADIENT IN RANA TEMPORARIA

Anssi Laurila [1], Beatrice Lindgren [1], Ane T. Laugen [2]

[1] *Uppsala University, Dept of Ecology and Evolution, Norbyvägen 18D, 75236, Uppsala, Sweden*
[2] *IFREMER, Laboratoire Ressources Halieutiques, Avenue du Général de Gaulle, BP 32, 14520, Port-en-Bessin, France*

anssi.laurila@ebc.uu.se

Increased predation rate is predicted to be one of the major costs of rapid growth rates. Since growth rates of ectotherms often increase towards higher latitudes and altitudes, high latitude populations should be more vulnerable to predation. We studied tadpole activity, vulnerability to predation and competitive ability in common frog *Rana temporaria* populations collected along a 1500 km latitudinal gradient across Scandinavia in common garden experiments, and compared predator densities between *R. temporaria* breeding ponds situated at low and high latitudes. Activity and foraging generally increased with latitude. While all populations responded to predator presence by decreasing activity and foraging, high latitude populations maintained higher activity levels in the presence of the predator. High latitude tadpoles experienced higher mortality than those from the low latitudes in the presence of free-ranging predators. In the wild, predator densities were significantly lower in high than in low latitude breeding ponds. Our results suggest that the trade-off between rapid growth and predation risk has been a significant factor in adaptive divergence along the latitudinal gradient.

06-06 Poster

CO-MIMICS HAVE A MUTUALISTIC RELATIONSHIP DESPITE UNEQUAL DEFENCE LEVELS

Hannah M. Rowland [1], Eira Ihalainen [2], Leena Lindström [2], Johanna Mappes [2], Michael P. Speed [1]

[1] University of Liverpool,, School of Biological Sciences, Biosciences Building, Crown Street,, L69 7ZB, Liverpool, United Kingdom
[2] University of Jyväskylä, Department of Biological and Environmental Science, Survontie 9, 40014, Jyväskylä, Finland

lilema@cc.jyu.fi

In the first clear mathematical treatment of natural selection, Müller proposed that a shared warning signal (mimicry) would benefit defended prey species by sharing out the per capita mortality incurred during predator education. Though mimicry is a mainstay of adaptationist thinking, whether there is a mutualistic or a parasitic relationship between unequally defended co-mimic species has been repeatedly debated. Here we examined this question in a "novel world" of artificial prey with a visually hunting predator (the wild great tit, Parus major). We kept the abundance of a highly defended prey ("Model") constant and increased the density of a moderately defended prey ("Defended Mimic") of either perfect or imperfect mimetic resemblance to the Model. Both co-mimics showed a net benefit from a density dependent decrease in their per capita mortality. Even when the effect of dilution through density was controlled for, Defended Mimics did not induce attacks on the model thus showing no parasitic effect. We did find that there was selection for accurate signal mimicry; both Models and Defended Mimics paid increased costs with imperfect mimicry. In comparison, the addition of fully Edible Mimics (Batesian mimics) did increase attacks on the Model (acting parasitically). However, this too was compensated for by the dilution effect through increased density; the Model suffered no overall increase in per capita mortality from Batesian mimicry. By ignoring the effects of density, current theories may have over-estimated the parasitic costs imposed by less defended mimics on highly defended models.

06-07 Poster

WATERBORNE PREDATOR CUES ELICIT DIFFERENTIAL ANTI-PREDATOR RESPONSES IN WILD TRINIDADIAN GUPPIES

Sanna Nilsson [1], Indar W. Ramnarine [2], Lars B. Pettersson [1]

[1] Lund University, Animal Ecology, Sölvegatan 37, 22362, Lund, Sweden
[2] University of West Indies, Life Sciences, St. Augustine, Trinidad & Tobago

sanna.nilsson@zooekol.lu.se

Predation is a strong selective force in most natural systems, commonly resulting in strong direct as well as indirect effects on prey. Central to these interactions is the degree to which prey are able to respond to the threat posed by predators and in particular how they make use of the cues available to them. Recent work in aquatic systems has demonstrated the importance of waterborne cues as a key element in predator recognition by prey. The degree to which populations differ in this response has received much less attention and its impact on prey mating behaviour has until now remained essentially unknown. In the present study, we have investigated the effect of sympatric and allopatric predator cues on mating behaviour and schooling in two populations of guppy, *Poecilia reticulata*, experiencing contrasting predation pressure. Using a laboratory design with wild-caught fish from Upper Aripo (low predation) and Lower Aripo (high predation) we demonstrated strong responses to two main predator species, *Crenicichla frenata* and *Rivulus hartii*, in fish from both sites, despite low predation fish having no prior experience of *C. frenata*. Cues from both predators elicited strong anti-predator behaviour (increased schooling) and affected mating behaviour by significantly reducing the frequency of male courting while not affecting the frequency of sneaky mating attempts. Predator size and diet were standardised to avoid prey responses being affected by cue concentration. Nevertheless, both guppy populations responded most strongly to cues from the fiercest predator, *C. frenata*. Our results demonstrate that wild guppies have the ability to respond to chemical cues from sympatric as well as allopatric predators, that they differentiate between different predators, and that mating behaviour is affected indirectly by such cues.

06-08 Poster

MAINTENANCE OF COLOUR POLYPHENISM IN LARVAE OF A MOTH SPECIES

Siiri-Lii Sandre [1], Toomas Tammaru [1], Toomas Esperk [1], Alo Vanatoa [2]

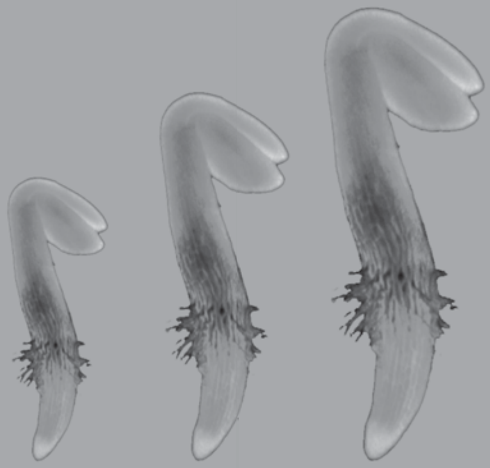
[1] *University of Tartu, ZHI, Vanemuise 46, 51014, Tartu, Estonia*
[2] *Estonian University of Life Sciences, Institute of Agricultural and Environmental Sciences, Fr.R. Kreutzwaldi 64, 51014, Tartu, Estonia*

siiri-ly@ut.ee

The lymantriid moth Orgyia antiqua has larval colour morphs that vary from the classical aposematic combination of black and yellow to dull black and brown. The coexistence of multiple colour morphs in aposematic species calls for an explanation, because warning signals should be monomorphic to reduce costs of schooling predators. The aim of the study was to empirically evaluate different potential explanations to the maintenance of the polyphenism. We tested if the polyphenism is maintained by proximate effects of diet, carotenoid-based biochemical trade-offS, thermal adaptation or bird predation. Even if the heritability of hair colour was low, no directional responces to environmental variables could be detected. However, the frequency of colour morphs correlated with body size: medium-sized larvae are conspicuously black and yellow and large ones are dull. The described pattern of colour change may be caused by a size-dependent trade-off between detectability and acceptability to bird predators. However, there was also an intriquing interaction between body size and colouration in determining detectability which could alone explain the observed patterns.

7

Game theory in an ecological context



Thursday August 23

Location: Ekonomikum 4

Symposium 7: Game theory in an ecological context

ORGANIZERS: Eva Kisdi, University of Helsinki, Finland
Hanna Kokko, University of Helsinki, Finland

9.45-10.15	**Olof Leimar** (invited) Phenotypic polymorphism, modifier evolution, and the fine-tuning of reaction norms
10.15-10.45	**John McNamara** (invited) The importance of individual differences in conflict and the evolution of cooperation
10.45-11.05	**Max Wolf** Life-history variation and the evolution of animal personalities
11.05-11.35	*Coffee*
11.35-11.55	**Michael Kopp** Competitive sympatric speciation: Understanding the role of costs
11.55-12.15	**Dan Cohen** Age dependent competitive learning rate game in demographic turnover populations of foraging bees, determined by depleting nectar levels in exploited flowers
12.15-12.35	**Jean-Baptiste Ferdy** Evolution of cooperation and social hierarchy
12.35-12.55	**Eva Kisdi** Evolutionary branching and long-term coexistence of cycling predators
12.55-14.00	*Lunch*

07-01 Talk

PHENOTYPIC POLYMORPHISM, MODIFIER EVOLUTION, AND THE FINE-TUNING OF REACTION NORMS

Olof Leimar [1]

[1] *Stockholm University, Department of Zoology, 10691, Stockholm, Sweden*

olof.leimar@zoologi.su.se

Phenotypic polymorphism is a consequence of developmental plasticity, in which the trajectories of developing organisms diverge under the influence of cues. Environmental and genetic phenotype determination are two main categories of polymorphic development. Even though both may evolve as a response to varied environments, they are traditionally regarded as fundamentally distinct phenomena. They can however be joined into a single framework that emphasizes the parallel roles of environmental and genetic cues in phenotype determination. From the point of view of immediate causation, it is common that phenotypic variants can be induced both by environmental and by allelic variation, which is referred to as gene-environment interchangeability. From the point of view of adaptation, genetic cues in the form of allelic variation at a polymorphic locus can play a similar role as environmental cues in providing information to the developmental system about coming selective conditions. Both types of cues can aid a developing organism to fit its phenotype to selective circumstances. Evolutionary change of the developmental system can be regarded either as fine-tuning of a reaction norm (the response to environmental cues) or as modifier evolution (the response to genetic cues). The perspective of information in environmental and genetic cues can be used to produce testable hypotheses about phenotype determination in an ecological context and it represents a generalization of the concept of conditional strategy in game theory.

07-02 Talk

THE IMPORTANCE OF INDIVIDUAL DIFFERENCES IN CONFLICT AND THE EVOLUTION OF COOPERATION

John M. McNamara [1]

[1] *University of Bristol, Mathematics, University Walk, BS65BZ, Bristol, UK*

john.mcnamara@bristol.ac.uk

Game theoretical models often ignore differences between individuals. Using a series of examples I will demonstrate that such differences are not innocuous noise, but can fundamentally change the nature of a game. Difference can completely reverse the direction of evolution in a simple prisoner's dilemma game, and can interact with lifespan to determine how cooperative parents are with each other. Finally, differences in personality promote the need to be socially sensitive; and once individuals are socially sensitive, this can lead to the maintenance of differences.

07-03 Talk

LIFE-HISTORY VARIATION AND THE EVOLUTION OF ANIMAL PERSONALITIES

Max Wolf [1], G. Sander Van Doorn [2], Olof Leimar [3], Franz J. Weissing [1]

[1] *University of Groningen, Theoretical Biology Group, Kerklaan 30, 9751NN, Haren, The Netherlands*
[2] *Santa Fe Institute, 1399 Hyde Park Rd., NM 87501, Santa Fe, USA*
[3] *Stockholm University, Department of Zoology, SE-106 91, Stockholm, Sweden*

m.wolf@rug.nl

Personalities are not restricted to humans but extend to a broad range of animal species: Individuals differ consistently in their behavioural tendencies and the behaviour in one context is correlated with the behaviour in multiple other contexts. Here we show how such personalities can evolve through natural selection. We focus on a scenario where the trade-off between current and future reproduction gives rise to a polymorphic population where some individuals put more emphasis on future fitness returns than others. Using an evolutionary model we demonstrate that these differences in investment give rise to personalities. Heavily investing individuals, who have much to lose, evolve to consistently avoid risks in all kinds of situations, like confrontations with predators and aggressive encounters, while non-investing individuals evolve to be bold and aggressive.

07-04 Talk

COMPETITIVE SYMPATRIC SPECIATION: UNDERSTANDING THE ROLE OF COSTS

Michael Kopp [1], Joachim Hermisson [1]

[1] *Ludwig-Maximilian-University Munich, Department Biology II, Section of Evolutionary Biology, Grosshadernerstrasse 2, 82152, Martinsried, Germany*

kopp@zi.biologie.uni-muenchen.de

Competition is an important force driving ecological diversification both within and between species. Recently, much interest has focused on the idea that frequency-dependent competition may lead to sympatric speciation by promoting the evolution of assortative mating. However, such models have also been at the center of much controversy. One recurrent criticism states that evolution of assortative mating will be impeded if choosy females experience fitness costs (such as running the risk of not finding a suitable mate). However, to what extent costs of choosiness can prevent speciation is unclear so far.

We have recently analyzed a genetically simple model of competitive speciation, which provides a detailed mechanistic understanding of the various selective forces influencing the evolution of assortative mating. Here, we extend this model to include costs of choosiness. By use of invasion fitness analysis, we investigate the structural stability of our earlier findings with regard to different kinds of costs, including those that do or do not influence population dynamics and those that do or do not lead to sexual selection. We observe that the effect of costs depends not only on their strength, but also on their type and, in particular, on whether they act primarily at low or at high levels of choosiness. Our results explain some of the conflicting findings about the importance of costs in the previous literature.

07-05 Talk

AGE DEPENDENT COMPETITIVE LEARNING RATE GAME IN DEMOGRAPHIC TURNOVER POPULATIONS OF FORAGING BEES, DETERMINED BY DEPLETING NECTAR LEVELS IN EXPLOITED FLOWERS

Dan Cohen [1]

[1] *The Hebrew University Jerusalem, Evolution Systematics Ecology, ESE Dept. The Hebrew University, 91904, Jerusalem, ISRAEL*

dancohen@vms.huji.ac.il

The interactions are modeled between the rate dynamics of age dependent sampling and learning by foraging solitary bees, the demographic turnover in the bee population, and the dynamics of nectar secretion and depletion in different flower species. Learning rates of preferences between flower species is proportional to the ratio between their average nectar yields. A steady state demographic turnover of the bee population is assumed, with a constant life span. The model defines the joint competitive steady-states of the learned age-dependent foraging preferences of the bees for different flower species, and the resulting steady state distribution of nectar in the flowers. Increasing the life time learning rate decreases the deviation between the nectar levels in different new flower species, which provides the benefit and motivation for sampling and learning. The decreased deviation between the flower species causes a negative feedback which decreases the learning rate in the population. Rare flower species are expected to deviate more than common species. New flower species are expected to be underutilized during learning transients, while familiar species with declining nectar production are expected to be overutilised.

07-06 Talk

EVOLUTION OF COOPERATION AND SOCIAL HIERARCHY

Jean-Baptiste Ferdy [1], Bernard Godelle [1]

[1] *Université Montpellier 2, ISEM - CNRS UMR 5554, 34095, Montpellier, France*

ferdy@univ-montp2.fr

The evolution of cooperation is impossible in a Darwinian context unless individual's and group's interests are positively correlated. Such a correlation can arise either because of some form of punishment against non-cooperative strategies, or because individuals of the group are related. Here we study a model where individuals compete for resources. The population is structured into classes, competition between classes being asymmetric: each individual has access only to the fraction of the resources that individuals of higher rank have left. Individuals are characterized by the fraction of available resource they take. We present here the evolutionary dynamics of this individual trait.

The expected outcome of selection in this model is that individuals should be selected to take as much resource they can, which yields a strongly skewed distribution of resources among individuals. This is indeed what happens when individuals' rank are randomly assigned at each generation. However, when ranks are strictly inherited from parents, the trait that determines what fraction of resources an individual takes becomes neutral. Moreover, when individual fitness increases slower than linearly with available resources, we found that selection can decrease the fraction of available resources taken by each individual. This makes the distribution of resources among individuals less skewed. We show that this is due to a form of kin selection where families compete to send offspring in higher classes. We then discuss these results in the context of human populations.

07-07 Talk

EVOLUTIONARY BRANCHING AND LONG-TERM COEXISTENCE OF CYCLING PREDATORS

Eva Kisdi [1]

[1] *University of Helsinki, Department of Mathematics and Statistics, PO Box 68, FIN-00014, Helsinki, Finland*

eva.kisdi@helsinki.fi

In most ecologically realistic scenarios, fitness of a phenotype depends on the presence and abundance of other phenotypes in the population. Classic evolutionary game theory centred on frequency-dependent selection, but it usually suppressed the effect of population size, and hereby implicitly assumed that population size is fixed. In reality, the size of most populations fluctuates. It is well known that population cycles and other types of non-equilibrium dynamics can facilitate species coexistence, but the evolutionary implications of frequency- and density-dependent selection in non-equilibrium systems are largely unexplored. In this presentation, I investigate whether coexisting predators may evolve from a single ancestor, and whether the coexistence of closely related predators is evolutionarily stable, when the predator-prey system undergoes population cycles. In particular, I assume that predator strategies differ in their handling times, because this trait has the largest influence on species coexistence. Longer handling times are costly in terms of lost foraging time, but allow the predator to extract more nutrients from the prey and therefore to produce more offspring per consumed prey. In the analysis, I apply the new method of critical function analysis to accommodate arbitrary trade-off functions between handling time and offspring production. I find that evolutionary branching of handling time is possible but not very likely; in contrast, evolutionarily stable coexistence of predators occurs under less restrictive conditions.

07-01 Poster

EVERYTHING YOU ALWAYS WANTED TO KNOW ABOUT SEX RATIO EVOLUTION BUT WERE AFRAID TO ASK

Krzysztof Argasinski [1]

[1] *Jagiellonian University, Biology and Earth Sciences-Institute of Environmental Sciences, Gronostajowa 7, 30-387, Cracow, Poland*

argas1@wp.pl

In a classical theory of sex ratio evolution (**sex ratio game**), grandchildren number is treated as a fitness measure of a female. The theory predicts that it is more profitable to produce offspring of the less numerous sex. We can find in literature mutually exclusive conclusions based on this prediction: some textbooks call 0.5 sex ratio as ESS, and others identify this ratio as a stable state of a population with different individual strategies being allowed. It is also not clear whether primary or secondary sex ratio is a target of evolution. Also, classical theory produces clear predictions only in the case of homogenous populations with an invading mutant and ignores important role of males, who host non-expressed sex ratio genes. The effect is that classic theory makes few false predictions. A new approach based on **multipopulation dynamic evolutionary games** clearly shows, that in populations diversified by individual strategies, population secondary sex ratio converges to the current value of primary sex ratio, which slowly converges to the unique stable value 0.5. Differences in mortality between sexes cause bias in secondary sex ratio. Surprisingly current proliferation of the gene, coding individual female strategy depends on sex ratio in subpopulation of the hosts of this gene (not on strategy coded by this gene) versus current population sex ratio. But the value of coded strategy affect the equilibrium value of sex ratio in the host subpopulation. As a result, all subpopulations approach rapidly their equilibria dependent on current population state, and then whole population slowly converges to global population stable state. This kind of dynamic equilibrium is a new generalization of ESS concept, called **Evolutionarily Stable System (ESSystem)**.

07-02 Poster

EVOLUTION OF DENSITY DEPENDENT DISPERSAL AND UNATTAINABLE EVOLUTIONARILY STABLE THRESHOLD DISPERSAL

Lars A. Bach [1], Jörgen Ripa [1], Per Lundberg [1]

[1] *Lund University, Theoretical Ecology, Sölvegatan 37, 223 62, Lund, Sweden*

lars.bach@teorekol.lu.se

For unconditional dispersal, the evolutionarily stable strategy (ESS) in terms of dispersal rate has been expressed as a function of dispersal cost, environmental variability and kinship. Likewise, the ESS for density dependent dispersal has been found to be a threshold response, i.e. the dispersal probability -the reaction norm- is a step function of density. For various levels of environmental variance and dispersal cost we let a two-parameter sigmoid reaction norm evolve in an individual-based model and found that a density dependent response is favoured over an unconditional response in the course of evolution. However, in our model the evolutionary end point tends towards soft density response rather than threshold dispersal. We propose that after a moderate density response has evolved selection levels off and drift prevents the population from reaching threshold dispersal, although it may be the ESS. In many natural populations such patterns may be expected for evolving life history traits subject to frequency dependent selection.

07-03 Poster

MODELLING BEHAVIOURAL SYNCHRONIZATION.

Iva Dostalkova [1]

[1] *University of South Bohemia, Faculty of Biological Sciences, Branisovska 31, 370 05, Ceske Budejovice, Czech Republic*

dost@bf.jcu.cz

Animals sharing common space often benefit from behavioural synchronization i.e. from making a behavioural switch at the same time. But in the group of N animals ideal times for the switches are usually different. Therefore there is the trade-off between the need to synchronize and the need to stick to the individually ideal time. In the model presented here we have N (or infinite number) of animals with N or (infinite number) of optimal switch times. Each animal can switch its behaviour independently on other animals, or it can synchronize its switch with another animals. We maximize the benefit function B of animal with respect to three parameters: b (waiting for the switch in non-synchrony switch), c (deviation from the optimal switch point in case of synchronization after optimal switch point), d (deviation from the optimal switch point in case of synchronization before optimal switch point). The optimal value of B depends on Q (penalization for non-synchrony), L (penalization for deviating by a time unit from the ideal time) and w (a coefficient expressing whether acting too early or acting too late is penalized more heavily). For a majority of the parameters Q/L the optimal strategy is synchronization before the ideal time ($c = 0$). Only when the penalization for non-synchrony is moderate to heavy (Q/L relatively large) and acting too early is penalized more than acting too late (w low) a mixed synchronization of ($c > 0$, $d > 0$) becomes optimal.

07-04 Poster

A MODEL FOR THE EVOLUTION OF MONOGYNY IN SPIDERS

Lutz Fromhage [1], John M. McNamara [2], Alasdair I. Houston [1]

[1] *University of Bristol, Dept. of Biology, Woodland Road, BS8 1UG, Bristol, UK*
[2] *University of Bristol, Dept. of Mathematics, University Walk, BS8 1TW, Bristol, UK*

lutzfromhage@web.de

Sexual selection theory predicts that males should attempt to mate with several females, unless the benefits of male promiscuity are trumped by alternative benefits associated with male monogamy (monogyny). Here we use a game theory model to address the adaptive value of a monogynous strategy which has the sole benefit of enhancing a male's paternity share in the context of competition with other males. We consider two ways in which monogynists might enhance their paternity: by out-competing rival ejaculates in sperm competition, and by reducing the probability that a female remates with rival males. The model is based on the biology of certain spiders, in which males are morphologically restricted to mate with either one or at most two females in their lifetime. Our results suggests that, regardless of the mechanism of paternity enhancement involved, a male-biased sex ratio is of primary importance for the evolution and maintenance of monogyny. Moreover, we show that there are large regions of parameter space where monogyny and bigyny can coexist as alternative mating strategies under stabilising selection. Our results are in qualitative agreement with empirical findings in spiders, and may also apply on a wider taxonomic scale.

07-05 Poster

GAME-THEORETIC MODELLING OF THE BREEDING SUPPRESSION HYPOTHESIS (BSH) AS A EVOLUTIONARILY STABLE STRATEGY

Sebastian Germerodt [1], Stefan Halle [1]

[1] *FSU Jena, Institute of Ecology, Dornburger Strasse 159, 07743, Jena, Germany*

Sebastian_Germerodt@web.de

The Breeding Suppression Hypothesis (BSH) describes the behaviour of female voles in northern Fennoscandia, which suppress reproduction due to the olfactorial perception of specialized mustelides. Females showing breeding suppression have a higher probability to survive the breeding season and benefit from a safer breeding season in the next year (Ylönen et al. 1994). Field experiments have shown that females, which were in the second year of reproduction, also suppress breeding. However, since it is very unlikely to survive another winter, a gain of fitness can only be achieved through reproduction. This could be evidence that fitness-payback is not - or not only - a consequence of low density after the winter, but an effect of the predator dynamics and patch-use-behaviour. Consequently, breeding suppression could be a duck and cover strategy (Fülling and Halle 2003). Suppressing females should have an equal or higher fitness output than breeding females in the absence of season effects like the very high winter mortality. To test this hypothesis we consider a model based on the Hawk-Dove-Game (Smith 1983). Suppressed breeding obviates lactation and requires lower foraging, compared to breeding females. Thus reduces the activity of suppressing females in the patch and, with a by chance acting predator, the predation-risk. The difference in predation probability forms a frequency dependent advantage. The model-setup compares fitness-values of a mixed population with two solitary populations playing only one strategy. First investigations show that females representing the Breeding Suppression Strategy have higher fitness values than breeding females, even in the absence of season effects. With further runs we intend to demonstrate that the predator dynamics mainly influence the fitness relation between the two strategies.

07-06 Poster

HOW TERRITORIALITY EVOLVES (AND HOW IT DOESN'T)

Martin Hinsch [1], Jan Komdeur [1], Ido Pen [2], Franz J. Weissing [2]

[1] University of Groningen, Animal Ecology, P.O.Box 14, 9750AA, Haren, Netherlands
[2] University of Groningen, Theoretical Biology, P.O.Box 14, 9750AA, Haren, Netherlands

m.hinsch@rug.nl

Territoriality is a classical topic of behavioural biology. Still, the evolutionary reasons for territorial behaviour are not well understood.

Recently simple models based on local interactions between individuals have been used to show that avoiding encounters is adaptive when sharing space is costly. From this it has been concluded that territoriality evolves under high fighting costs whereas low fighting costs result in overlapping home ranges.

I will present new modelling results that indicate that the situation is considerably more complicated. We first extended the previous approach which compared the invasion prospects of four discrete strategies by letting the behaviour of individuals dynamically evolve on a continuous range of strategies. It turns out that in the extended model the general pattern of increased sharing with decreasing costs remains. At the same time however many different spatial patterns of space use evolve. Only few of these are easily classifiable as either territorial or non-territorial. Then we relaxed the assumption of fixed fighting costs by making the decision to fight an intruder evolvable. This leads to the disappearance of territorial behaviour in most cases. In our opinion these results reveal some basic flaws in the assumptions of the previous model as well as the definition of territoriality used.

With an improved model we show that it is important how the costs of sharing arise - through interference or fights, how resources are distributed and renewed and how information about claims of ownership is transmitted in the population. Finally the choice of strategy space, i.e. which different behavioural strategies individuals are assumed to be able to choose from has a considerable influence on the outcome of evolution.

07-07 Poster

USING EVOLUTIONARY ALGORITHMS TO MODEL ECOLOGIES AND EVOLUTION

Jan T. Kim [1]

[1] University of East Anglia, School of Computing Sciences, University Plain, NR2 3BZ, Norwich, United Kingdom

jtk@cmp.uea.ac.uk

The process of natural evolution has inspired Evolutionary Algorithms (EAs), which use partial models of evolution to heuristically solve nontrivial optimisation problems. EAs operate by maintaining populations of candidate solutions to the optimisation problem and repeatedly subjecting selection, biased by fitness values (which reflect a candidate solution's performance in solving the problem), mutation and crossover. EAs have much potential as computational models of evolution. The fitness function in an EA modelling biological evolution should reflect interactions among co-evolving individuals within a population or an ecosystem. This is realised in LindEvol, a framework which uses a simulation of plants growing in a shared environment, incorporating energy flux and nutrient cycles.

Evolution of complexity is bounded by the well-known error threshold, i.e. a critical value of the mutation rate. Adaptive mutation rates, an element introduced by evolution strategies (a classical type of EA) can help keep the level of complexity evolved by an EA flexible, but they can also result in loss of diversity in the evolving population.

Adaptation of mutation rates, e.g. by proofreading mechanisms, is linked to a cost (in terms of energy and other resources) in biological evolution. This has been incorporated in LindEvol by linking mutation rate adaptation to an energy cost. The resulting simulations demonstrate that this energy cost is an important mechanism for maintaining genetic diversity while enabling adaptive evolution.

LindEvol was used to assess methods for measuring biodiversity. The results of this study demonstrate that genetic information provides a good basis for quantifying biodiversity. In contrast to this, biodiversity measures based on true phylogenetic trees, directly extracted from EA runs, are shown to be insensitive to major evolutionary changes in biodiversity.

Some of this work is published. Information on LindEvol can be found at http://www.cmp.uea.ac.uk/~jtk/lindevol/ .

07-08 Poster

FROM INFANTICIDE TO PARENTAL CARE: WHY SPATIAL STRUCTURE CAN HELP ADULTS BE GOOD PARENTS

Sébastien Lion [1], Minus Van Baalen [1]

[1] École normale supérieure/Université Pierre et Marie Curie - Paris 6/CNRS, UMR 7625 "Fonctionnement et évolution des systèmes écologiques", Bât A - 7e étage - CC 237 - 7, quai Saint-Bernard, 75005, Paris, France

slion@biologie.ens.fr

Over the last twenty years, the role of spatial self-structuring as a template for evolution has drawn much attention. Spatial structure can be an important component of the feedback loop between ecology and evolution: the evolution of a trait (e.g. migration, altruism) can shape the local structure of the population, which in turn creates new selective pressures on the evolving trait. As a consequence, the evolution of spatially-structured populations often displays very different features from the evolution of well-mixed populations. The main goal of this talk is to review some of these key features using the evolution of parental care as an example. Using a combination of correlation equations (also known as pair approximation) and adaptive dynamics, we investigate the evolution of parental care and cannibalism in a spatially-structured population where adults can either help or kill juveniles in their neighbourhood. We show that spatial structure can reverse the selective pressures on adult behaviour, leading to the evolution of parental care; whereas the non-spatial model predicts that cannibalism is the sole evolutionary outcome. We briefly discuss how the shape of the trade-off between adult reproduction and parental care can affect the long-term evolutionary ouctome. Our analysis emphasizes that evolution of such spatially-structured populations is best understood at the level of the cluster of invading mutants, and we define invasion fitness as the growth rate of that cluster. We derive an analytical expression for the selective pressures on the trait, and show that relatedness and Hamilton's rule in class-structured populations are recovered as emergent properties of the spatial ecological dynamics. We discuss the links between our work and classical kin selection models, and argue for a different approach to correlation equations in evolutionary ecology.

07-09 Poster

FREQUENCY-DEPENDENT SELECTION ON BEHAVIOURAL STRATEGIES

Tapio Mappes Mappes [1], Jouni Aspi [2], Esa Koskela [1], Tanja Poikonen [1], Juha Tuomi [3]

[1] University of Jyväskylä, Biological and Environmental Science, P.O. Box 35, FIN-40014, Jyväskylä, Finland
[2] University of Oulu, Biology, P.O. Box 3000, FIN-90014, Oulu, Finland
[3] University of Oulu, Biology, P.O. Box 333, FIN-90571, Oulu, Finland

tmappes@bytl.jyu.fi

Negative frequency-dependent selection, which favours rare genotypes, has suggested to be an important evolutionary mechanism maintaining genetic variation in populations. Here we tested the assumptions and predictions of the model presented by Tuomi et al. (Behav. Ecol. Sociobiol, 40:227-233, 1997), where evolutionary stability of bavioural strategy (female infanticide) was analysed in a game-theoretical context. First we show evidence for the main assumption; the existence of genetic tactics in our study populations of bank voles Myodes glareolus. Then we experimentally showed that the frequency of infanticide tactic in the populations is maintained by the resource benefits gained by the infanticidal individuals. These findings support the hypothesis of Tuomi et al (1997) that the resource benefits allowed an infanticidal strategy to invade a population of non-infanticidal individuals.

07-10 Poster

MULTILOCUS MODELS FOR THE EVOLUTION OF SOCIAL INTERACTIONS IN SPATIALLY STRUCTURED POPULATIONS

Denis Roze [1], François Rousset [2]

[1] *CNRS UMR 7144, Station Biologique de Roscoff, Place Georges Teissier, BP 74, 29682, Roscoff Cedex, France*
[2] *Université Montpellier II, Institut des Sciences de l'Evolution, Place Eugène Bataillon, cc 065, Montpellier Cedex 05, France*

roze@sb-roscoff.fr

Many evolutionary processes involve interactions among several genes. Furthermore, sex and recombination are widespread among eucaryotes. Despite this, the effects of gene interactions and recombination on social evolution have been little studied, as most game theoretical or kin selection models suppose asexual reproduction, or don’t explore the effects of the genetic architecture of traits. During the last years, we developped a general theoretical framework for constructing multilocus models of structured populations, that can be used to compute evolutionary stable strategies for games involving different coevolving genes, in a spatial context. The core of the method consists in writing expressions for changes in allele frequencies at different loci, as functions of genetic covariances between genes in different interacting individuals. A separation of timescales argument can then be used to reduce the number of variables. We used this methodology to treat different biological questions, involving the coevolution of altruism and the punishment of cheaters, the evolution of helping conditional on kin recognition, the effects on inbreeding depression on the evolution of dispersal rates, and the effects of population structure on the evolution of mating systems. During this talk I will give an overview of this methodology, and present some these applications. These illustrate the fact that the spatial structure of populations can have important effects on evolutionary processes.

07-11 Poster

THE EVOLUTION OF PHENOTYPE DETERMINATION

Claus Rueffler [1], Peter A. Abrams [1]

[1] *University of Toronto, Department of Ecology and Evolutionary Biology, 25 Harbord Street, M5S 3G5, Toronto, Canada*

rueffler@zoo.utoronto.ca

Many heterogeneous environments favour different phenotypes in different places or at different times. Phenotypic diversity can either result from genetic diversity of from a single genotype capable of producing different phenotypes. A single genotype might produce different phenotypes, for example in response to an environmental cue (phenotypic plasticity) or through a randomization mechanism (bet-hedging). A large part of the existing theoretical literature attempts to give conditions under which one of these specific mechanisms is favoured over a phenotypically monomorphic population. However, in many circumstances different evolutionary responses are favoured simultaneously and the real question becomes which of these different responses might evolve first and possibly pre-empt any selection driving one of the alternative responses. We will address this question by analysing a lottery-model incorporating temporal heterogeneity and environmental cues. Our results show that in large part of the parameter space neither pure bet-hedging nor pure plasticity is favoured but a combination of the two. It also possible that a genetic polymorphism evolves in traits that determine the phenotypic variance of bet-hedging and plastic genotypes.

07-12 Poster

HUMAN COOPERATION AND THE USE OF GOSSIP

Ralf D. Sommerfeld [1], Hans-Juergen Krambeck [1], Dirk Semmann [2], Manfred Milinski [1]

[1] Max Planck Institute for Evolutionary Biology, Dept. of Evolutionary Ecology, August-Thienemann-Strasse 2, 24306, Ploen, Germany
[2] University of Vienna, Institute for Mathematics, Nordbergstrasse 15, 1090, Vienna, Austria

sommerfeld@mpil-ploen.mpg.de

Game theory is a unique tool to investigate and analyse complex social problems. It has also been used to explain the evolution of human cooperation. Therein, one focus traditionally lays on pairwise encounters between members of a population. One individual acts as a donor, whereas the other as a recipient. In mathematical models (Nowak & Sigmund 1998, Nature) as well as in experimental studies (e.g. Milinski, Semmann, Krambeck 2002, Nature) it has been shown that individuals that help others are also being helped, whereas those that do not receive less or nothing.

The problem of these studies is, however, that individuals have access to information based on direct observation. In natural situations, it is impossible for an individual to observe all those individuals it possibly interacts with in the future. Therefore, many authors suppose that in nature direct observation is replaced by gossiping (e.g. Enquist & Leimar 1993, Anim. Behav.; Nowak & Sigmund 1998, Nature; Panchanathan & Boyd 2003, JTB). In our study we investigated the use of gossip for the first time in a cooperation context. Similar to Milinski et al.'s study, we analysed the behaviour of University students in a computer based game.

We found that information transfer via gossip dampens the resulting cooperation compared to cooperation levels based on direct observations. Nonetheless, gossip might indeed be an alternative to direct observation. Furthermore, we found that people are influenced by gossip, even if they have access to direct information (via observation). This fact documents a strong manipulative potential of gossiping.

07-13 Poster

THE EVOLUTIONARY STABILITY OF AUTOMIMICRY

Thomas O. Svennungsen [1], Øistein H. Holen [1]

[1] University of Oslo, CEES, Department of Biology, P.O.Box 1066, Blindern, N-0316, Oslo, Norway

t.o.svennungsen@bio.uio.no

Internal defences such as toxins cannot be detected from a distance by predators, and are likely to be costly to produce and maintain. Populations of well-defended prey may therefore be vulnerable to invasion from rare 'cheater' mutants that do not produce the toxin themselves but obtain some protection because of their resemblance to their better defended conspecifics (automimicry). Automimicry may thus explain the large intraspecific variation often observed in defence levels. Although it is well established that well-defended and weakly defended morphs may coexist stably in protected dimorphisms, previous theoretical work has suggested that such dimorphisms would not be resistant to invasion by novel mutants with defence levels intermediate to those present. Given that most defences (including toxins) are likely to be continuous traits, this implies that automimicry may tend to be a transitory phenomena, and thus less likely to explain the variation in defence levels in nature. Using a game theoretic approach we show that automimicry can indeed be evolutionarily stable also for continuous traits, and that it may evolve under a wide range of conditions. We further employ a geometric method recently developed in the field of adaptive dynamics, which allows us to use a trade-off curve to directly determine whether an evolutionarily stable defence dimorphism is possible, and if so, the component strategies that might comprise it. This method also enables us to make some qualitative inferences about the ecological conditions that favour the evolution of automimicry.

07-14 Poster

REINTERPRETING BET-HEDGING USING RELATIVE FITNESS

Francisco Úbeda [1], Alan Grafen [1]

[1] *Oxford University, St John's College, St John's College, OX1 3JP, Oxford, UK*

francisco.ubeda@sjc.ox.ac.uk

In the seventies theoretical work showed that the maximization of arithmetic mean fitness could not explain the evolution of organisms in stochastic environments. It was geometric mean fitness maximization that explained their evolution. The interpretation of such result was that organisms are selected to strike a balance between risk and fitness. Arithmetic mean fitness is insensitive to fitness variance but this is not the case of geometric mean fitness whose optimal value strikes the right balance between fitness and fitness variance. Such balance was termed bet-hedging following the use made in the financial literature. This compelling interpretation rapidly spread in the ecological literature. Insect diapause, seed dormacy, clutch size or virus latency have all been explained in terms of bet-hedging.

Recent work questions not only that geometric mean fitness is the right maximand for organisms in stochastic environments but also the outcome's interpretation in terms of balance between arithmetic mean fitness and variance. Within his Formal Darwinism Project Grafen provides an all encompassing way of defining fitness that accounts for both deterministic and stochastic environments. Grafen provides a simple yet powerful way to reconcile adaptation in deterministic and stochastic environments.

In this research we start by providing a formal definition of bet-hedging as used in the biological literature. We further explain the implications of the proper definition of reproductive value in stochastic environments. We review the biological literature on bet-hedging and classify all cases in three different groups according to the definition of bet-hedging that corresponds to each example. We extend Grafen's definition when necessary. We conclude that all systems in which the role of bet-hedging has been acknowledged can be explained without having to recur to trade-off between fitness and variance.

07-15 Poster

THE EVOLUTION OF HANDEDNESS IN SCALE-EATING CICHLIDS

Tom J. M. Van Dooren [1], Henk Van Goor [1], Maaike Van Putten [1]

[1] *Leiden University, Institute of Biology, Kaiserstraat 63, 2311GP, Leiden, Netherlands*

t.j.m.van.dooren@biology.leidenuniv.nl

The handedness polymorphism in the cichlid *Perissodus microlepis* is a classic example of a polymorphism which probably originated by frequency-dependent disruptive selection. Right-handed fish preferably rip scales from the left flank of prey fish, left-handed fish from the right flank. A rarity advantage can occur when prey guard their flank which is more often attacked better.

Handedness is supposed to be determined by a major gene, with a dominant gene coding for right-handed beak orientation. By means of an evolutionary model we show that alternative responses to disruptive selection are also likely. Populations can evolve to consist of right- (left-) handed fish exclusively, or another alternative is that developmental instability is favoured without a major gene evolving.

In a lab population we therefore started investigating the determination of handedness and the association with preference for attacking either the left or the right flank of prey. The distribution of handedness asymmetry in our lab population is unimodal, not supporting the presence of a major gene. We were also able to change the beak orientation of individuals by forcing them to forage against their preference on the flank of our choice. This proves that beak orientation has a plastic "environmental" component. Our results demonstrate that further study of handedness determination is warranted. We are now trying to breed the scale-eaters, so that we can estimate genetic components of handedness variation.

07-16 Poster

FIXATION PROBABILITY FOR A BENEFICIAL ALLELE AND A MUTANT STRATEGY IN A LINEAR GAME UNDER WEAK SELECTION IN A FINITE ISLAND MODEL

Véronique Ladret [1], Sabin Lessard [1]

[1] *Université de Montréal, Départenment de mathématiques et de statistique, C.P. 6128 Succursale Centre-ville,, H3C 3J7, Montréal (QC), Canada*

ladretve@dms.umontreal.ca

The effect of population structure on the probability of fixation of a newly introduced mutant under weak selection is studied using a coalescent approach. Wright's island model in a framework of a finite number of demes is assumed and two selection regimes are considered : a beneficial allele model and a linear game among offspring. A first-order approximation of the fixation probability

for a single mutant with respect to the intensity of selection is deduced. The approximation requires the calculation of expected coalescence times, under neutrality, for lineages starting from two or three sampled individuals. The results are obtained in a general setting without

assumptions on the number of demes, the deme size or the migration rate, which allows for simultaneous coalescence or migration events in the genealogy of the sampled individuals. Comparisons are made with limit cases as the deme size or the number of demes goes to infinity or the migration rate goes to zero for which a diffusion approximation approach is possible. Conditions for selection to favor a mutant strategy replacing a resident strategy in the context of a linear game in a finite island population are addressed.

07-17 Poster

ADAPTIVE DYNAMICS IN THE TRIVERS-WILLARD MODEL OF SEX EXPRESSION

Philipp L. Wesche [1]

[1] *University of Edinburgh, Institute of Evolutionary Biology, West Mains Road, EH9 3JT, Edinburgh, United Kingdom*

philipp.wesche@ed.ac.uk

Sex ratios influence the scope for sexual selection. This is particularly true of the Trivers-Willard model, which applies in situations of strong sexual selection, notably in polygynous species.

If we assume that females are the choosier sex, they can increase male fitness variance by selecting mates on the basis of genetic quality. It is then adaptive for genetically better offspring to be male, because female choosiness increases variation in fitness among males. This mechanism also affects the likelihood of, and time taken to, fixation for alleles that affect fitness. I present data showing the effect on beneficial, deleterious, and sexually antagonistic alleles, and suggest implications for adaptive evolution.

8

Integrating ecology and evolution: a synthesis

Friday August 24 *Location*: Ekonomikum 3

Symposium 8: Integrating ecology and evolution: a synthesis

Organizers: Nils Christian Stenseth, University of Oslo, Norway
Eli Rueness, University of Oslo, Norway

9.45-10.15	**Thomas Hansen** (Invited) Integrating ecology and evolution in the comparative method
10.15-10.45	**Loren Rieseberg** (Invited) Integrating ecology and evolution: an example from sunflowers
10.45-11.05	**Carol Eunmi Lee** Rapid evolution across independent invasions into novel environments
11.05-11.35	*Coffee*
11.35-11.55	**Daniel Nussey** Understanding the evolutionary ecology of phenotypic plasticity in the wild
11.55-12.15	**Helena Koivulehto** Adaptive radiation of forest dung beetles in Madagascar
12.15-12.35	**Virpi Lummaa** Sex ratio at birth affects reproductive success in humans
12.35-14.00	*Lunch*
14.00-14.20	**Daniel Berner** From local adaptation to ecological speciation: divergent selection and gene flow in the lake/stream stickleback system
14.20-14.40	**Jörgen Ripa** Adaptive dynamics in stochastic environments
14.40-15.00	**Daphne Fairbairn** Laboratory evolution of trade-offs 1: Testing predictions from quantitative genetics on the loss of dispersal capability
15.00-15.20	**Anna Qvarnström** Long-term fitness consequences of hybridization in Ficedula flycatchers
15.20-16.00	*Coffee*

08-01 Talk

INTEGRATING ECOLOGY AND EVOLUTION IN THE COMPARATIVE METHOD.

Thomas F. Hansen [1]

[1] *University of Oslo, Biology, PB 1066, Bllindern, 0316 Oslo, Norway*

thomas.hansen@bio.uio.no

Phylogenetic comparative methods are usually constructed to correct for non-independence among species. The models used to achieve this are mostly chosen for statistical convenience, and not for their biological assumptions. I will argue that the assumptions made in most standard comparative methods are plainly incompatible with adaptive evolution in ecological niches. I then discuss some recent process-based comparative methods that explicitly incorporate adaptation to an ecological niche, and can be used to estimate niche parameters. I illustrate their use with an analysis of thermophysiological adaptation, phylogenetic inertia, and niche tracking in Liolaemus, a genus of South American lizards living under diverse climatic conditions.

08-02 Talk

INTEGRATING ECOLOGY AND EVOLUTION: AN EXAMPLE FROM SUNFLOWERS

Loren H. Rieseberg [1]

[1] *University of British Columba, Botany, 3529-6270 University Blvd, V6T 1Z4, Vancouver, Canada*

lriesebe@interchange.ubc.ca

Plants provide extraordinary opportunities for linking ecology and evolution. They are a diverse group, and much of the diversification has occurred recently, creating spectacular examples of adaptive radiation and of "speciation in action." With the exception of their propagules, plants are sessile, facilitating ecological study. However, they vary dramatically in mating system, ploidal level, dispersal syndrome, and life history, aiding efforts to understand the contribution of various ecological and evolutionary factors to diversification. Here I show how the integration of ecological and evolutionary approaches in annual sunflowers has allowed us to (1) determine how new hybrid lineages arise and colonize novel habitats, (2) identify genes underlying the repeated evolution of weedy sunflower populations, and (3) and test a possible strategy for limiting the movement of genetically engineered genes from crop plants into their wild relatives.

08-03 Talk

RAPID EVOLUTION ACROSS INDEPENDENT INVASIONS INTO NOVEL ENVIRONMENTS

Carol Eunmi Lee [1]

[1] *University of Wisconsin, Center of Rapid Evolution, 430 Lincoln Drive, Zoology, 53706, Madison, USA*

carollee@wisc.edu

Of the large number of species that are introduced into novel habitats, few become successful as invaders. What allows some species to invade, when most cannot? We hypothesized that invasions into novel environments might involve the rapid and parallel evolution of genetically labile traits. Within the past century, the copepod Eurytemora affinis has invaded freshwater habitats multiple times independently from saline sources. To dissect evolutionary responses during these independent habitat invasions, we integrated analyses of physiological function (ion efflux and uptake) with comparative functional genomics (using custom cDNA microarrays). We analyzed evolutionary shifts during invasions for pairs of saline ancestral source and derived freshwater populations across four independent invasions from two genetically distinct clades. We found evolutionary shifts in the expression of genes spanning many functional categories, including osmoregulation and stress response. A diverse array of genes showed parallel shifts in gene expression across multiple independent invasions, while some genes showed parallelism only within clades. In particular, shifts in gene expression and physiological function suggested mechanisms to reduce ionic loss rather than to increase ion uptake in the derived freshwater populations. The integration of functional (physiological) and gene expression analyses has allowed us to prioritize plausible candidate genes that might serve as the targets of selection. The evolutionary parallelism observed here might have relevance for taxonomically different but ecologically similar species that invade across similar habitat clines.

08-04 Talk

UNDERSTANDING THE EVOLUTIONARY ECOLOGY OF PHENOTYPIC PLASTICITY IN THE WILD

Daniel H. Nussey [1], Alastair J. Wilson [2], Jon E. Brommer [3]

[1] *University of Cambridge, Department of Zoology, Cambridge, UK*
[2] *University of Edinburgh, Institute of Evolutionary Biology, Edinburgh, UK*
[3] *University of Helsinki, Dept. of Biological & Environmental Sciences, Helsinki, Finland*

dhn24@cam.ac.uk

Understanding how the environment influences phenotypic and genetic variation in nature represents an important step towards an integrated understanding of evolutionary and ecological processes. Populations are able to track changes in environmental conditions via two mechanisms: micro-evolution and phenotypic plasticity. Phenotypic plasticity, the ability of individual genotypes to alter their phenotype in response to environmental change, is likely to be fundamental to any population’s ability to deal with short-term environmental change. We currently know little about the prevalence, and evolutionary and ecological causes and consequences of variation in phenotypic plasticity in the wild. In this talk, I will briefly outline an analytical framework to assess the between-individual variation in life history plasticity that may underlie population-level responses to the environment at both phenotypic and genetic levels. This framework utilizes the reaction norm concept and random regression statistical models. Using examples of recent applications of the framework, from long-term individual-based studies of wild vertebrate populations, I will illustrate how both natural selection and ecological constraint may alter a population's response to the environment over time. These examples highlight the need to consider the ecological and evolutionary consequences of environmental change at the individual and genetic level in natural systems.

08-05 Talk

ADAPTIVE RADIATION OF FOREST DUNG BEETLES IN MADAGASCAR

Helena Wirta [1], Orsini Luisa [1], Ilkka A. Hanski [1]

[1] *University of Helsinki, Biological and Environmental Sciences, Viikinkaari 1 (P.O. BOX 65), 00014, Helsinki, Finland*

helena.koivulehto@helsinki.fi

Adaptive radiations of mammals have contributed to the exceptionally high levels of biodiversity and endemism in Madagascar. Dung beetles are dependent on mammals for their resources, dung and carrion. Here we examine the evolutionary history of an endemic dung beetle tribe Helictopleurini (Scarabaeidae) in Madagascar. We have reconstructed the molecular phylogeny of Helictopleurini and its putative sister tribes. Helictopleurini is monophyletic and most likely has a single origin, which we date at 37 to 23 MY, supporting overseas colonization of Madagascar. The main radiation of Helictopleurini occurred concurrently with the main radiations of lemurs, the most significant mammalian taxon for dung beetles in Madagascar. The ancestors are inferred to have been coprophagous species inhabiting open habitats. Subsequent evolution has involved shift into forests, changes in resource use to a more generalized diet, and changes in body size. Four species of the extant 65 species have shifted to use the dung of cattle, which was introduced to Madagascar about 1500 years ago. This transition has occurred independently three times, and the diet shift has allowed three species to greatly expand their geographical ranges in comparison with the forest-dwelling species, which typically have restricted ranges. In 8 of 9 sister species pairs the species have allopatric or parapatric distributions. The sister species are genetically strongly differentiated and hence have diverged a long time ago, with one exception, involving a potentially recent shift to cattle dung by one of the species. The closely related Onthophagini have colonized Madagascar several times, but they have not entered forests nor radiated in Madagascar, most likely because of competition with Helictopleurini in forests and the recent origin of abundant cattle dung in open areas.

08-06 Talk

SEX RATIO AT BIRTH AFFECTS REPRODUCTIVE SUCCESS IN HUMANS

Virpi Lummaa [1], Jenni E. Pettay [2], Andrew F. Russell [1]

[1] *University of Sheffield, Department of Animal and Plant Sciences, Western Bank, S10 2TN, Sheffield, United Kingdom*
[2] *University of Turku, Department of Biology, FIN-20014, Turku, Finland*

v.lummaa@sheffield.ac.uk

In mammals, including humans, female fetuses which are exposed to testosterone from adjacent male fetuses *in utero* can have masculinized anatomy and behavior. However, the reproductive consequences of such pre-birth sex-ratio effects for offspring and their implications for maternal fitness remain unexplored. Here we investigate the effects of being gestated with a male co-twin for daughter lifetime reproductive success, and the fitness consequences for mothers of producing mixed-sex twins in pre-industrial (1734-1888) Finns. We show that daughters born with a male co-twin have reduced lifetime reproductive success compared to those born with a female co-twin. This reduction arises because such daughters have decreased probabilities of marrying as well as reduced fecundity. Mothers who produce opposite-sex twins consequently have fewer grandchildren (and hence lower fitness) than mothers who produce same-sex twins. Our results are unlikely to be a consequence of females born with male co-twins receiving less nutrition, for such females do not have reduced survival and increases in food availability fail to improve their reproductive success. Nor are our results explained by post-birth social factors (females growing up with similarly-aged brothers), for females born with a male co-twin have reduced success even when their co-twin dies shortly after birth and are raised as singletons post-birth. Our findings suggest that hormonal interactions between opposite-sex fetuses known to influence female morphology and behavior can also have negative effects on daughter fecundity and hence maternal fitness, and bear significant implications for adaptive sex allocation in mammals.

08-07 Talk

FROM LOCAL ADAPTATION TO ECOLOGICAL SPECIATION: DIVERGENT SELECTION AND GENE FLOW IN THE LAKE/STREAM STICKLEBACK SYSTEM

Daniel Berner [1], Andrew Hendry [1]

[1] *McGill University, Dept. of Biology, 859 Sherbrooke St. W., H3A 2K6, Montreal, Canada*

daniel.berner@mail.mcgill.ca

Divergent selection imposed by ecological conditions that differ between environments frequently leads to local adaptation, but can further cause reproductive isolation that allows a lineage to split into new species (ecological speciation). Identifying factors that promote or constrain ecological speciation is most feasible where replicate study systems are available that differ in the factors of interest. We explore the roles of divergent selection and gene flow to ecological speciation in threespine stickleback fish from eight replicate watersheds in British Columbia, Canada. Each of these watersheds consists of a lake and a stream that drains from the lake, providing the opportunity for both ecologically-based divergent selection (lake vs. stream), and dispersal between the two habitats. In each watershed, we took seven clinal samples with 200 – 1500 m distance between the sites, starting at the lake and moving downstream. Our analysis integrates three sources of data:1) Phenotypic differentiation among localities in each watershed, as quantified with geometric morphometrics, 2) estimates of neutral divergence and immigration rates into local populations based on microsatellite variation, and 3) field measurements of key ecological variables (prey types and abiotic variables) that characterize local selective environments. So far, our analysis suggests that the studied watersheds form a continuum. On one end of this continuum are watersheds with a relatively high degree of dispersal between lake and stream sites. Here, we do find adaptation to lake and stream habitats, but the degree of adaptive divergence appears constrained by gene flow. On the other end of the continuum are watersheds characterized by strong divergent selection between lake and stream habitats. In this situation, the potential for gene flow rather than adaptive divergence seems limited, which allows the lake and stream populations to form distinct parapatric gene pools that are best viewed as incipient species.

08-08 Talk

ADAPTIV DYNAMICS IN STOCHASTIC ENVIRONMENTS

Jörgen Ripa [1], Ulf Dieckmann [2]

[1] *Lund University, Theoretical Ecology, Ecology Building, 223 62, Lund, Sweden*
[2] *International Institute for Applied Systems Analysis, Evolution and Ecology Program, A-2361, Laxenburg, Austria*

jorgen.ripa@teorekol.lu.se

The rate of gradual evolution of a single trait of a single population is predicted by the canonical equation of the adaptive dynamics famework. The canonical equation states that the rate of evolutionary change is proportional to the equilibrium population size as well as the invasion fitness gradient, as determined by the populations' current environment and intraspecific interactions. An underlying assumption of this theory is the common separation of ecological and evolutionary timescales, such that the population is assumed to reach ecological equilibrium much faster than the rate of evolutionary change. However, natural populations never reach equilibrium. Rather, a variable environment makes population size vary continuously over time. which may have consequences for evolution. To take this into account, we have derived corrections to the canonical equation, which incorporate a variable environment as well as the resulting population size fluctuations. The corrected canonical equation provides, for the first time, a general theory which bridges the gap between population dynamics and evolutionary dynamics. As an example, the theory can be used to investigate the evolution of dynamic stability of a single population. More interestingly, it can be generalized to multispecies co-evolution and community dynamics.

08-09 Talk

LABORATORY EVOLUTION OF TRADE-OFFS 1: TESTING PREDICTIONS FROM QUANTITATIVE GENETICS ON THE LOSS OF DISPERSAL CAPABILITY.

Daphne J. Fairbairn [1], Derek A. Roff [1]

[1] *University of California, Biology, 900 University Avenue, 92521, Riverside, United States*

daphne.fairbairn@ucr.edu

Predicting evolutionary change is the central goal of evolutionary biology because it is the primary means by which we can test evolutionary hypotheses. In this talk we analyze the pattern of evolutionary change in a laboratory population of the wing dimorphic sand cricket, *Gryllus firmus*, resulting from relaxation of selection favoring dispersal by flight. Based on our quantitative genetic analysis of the well-characterized trade-off between fecundity and flight capability in female *G. firmus*, we predict that evolution in the laboratory environment should result in a reduction in the proportion long-winged, increased fecundity in long-winged females, and reduced functionality and weight of the major flight muscles in long-winged females. Conversely, we predict little change in short-winged (flightless) females because they do not sacrifice fecundity for functional flight muscles. To test these predictions, we compare females from the first, second and approximately tenth generations of a population maintained in the laboratory with no opportunity for dispersal by flight (migration). Our results confirm that laboratory evolution has occurred in this population along the predicted trajectories and demonstrate the capacity for rapid adaptive evolution of migratory capacity in this species.

08-10 Talk

LONG-TERM FITNESS CONSEQUENCES OF HYBRIDIZATION IN FICEDULA FLYCATCHERS

Anna Qvarnström [1]

[1] *Uppsala University, Ecology and Evolution, Norbyv.18d, 75264, Uppsala, Sweden*

anna.qvarnstrom@ebc.uu.se

Few processes in nature may lead to as fundamentally different outcomes as hybridization between divergent taxa. Matings across species borders may lead to the breakdown of reproductive isolation between species, the build-up of reproductive isolation (reinforcement), or to the origin of novel species. These different possible scenarios to a large extent depend on the amount of gene flow, which in turn depends on a number of external (ecological) and internal factors (genetic compatibility). In order to capture the combined action of these factors I estimated the long-term fitness consequences of hybridization between pied and collared flycatchers in a natural hybrid zone. The obtained multi-generation estimate of selection against hybridization revealed that the estimated cost increased with the number of generations considered. There were both natural and sexual selection operating against hybrids and backcrosses. I discuss the possibility that the strength of post-zygotic isolation between closely related species may in general be underestimated

08-01 Poster

IDENTIFICATION OF GENES RELATED TO SPECIATION AND SPECIALIZATION IN THE PLANT-PATHOGENIC FUNGUS MICROBOTRYUM: POSITIVE SELECTION PATTERNS DETECTED UNDER A COMPARATIVE GENOMICS FRAMEWORK

Gabriela Aguileta [1], Tatiana Giraud [1]

[1] *Universite Paris-Sud, Genetique et Ecologie Evolutives, Bâtiment 360, 91405, Orsay, France*

gabriela.aguileta@u-psud.fr

At the molecular level, signatures of positive selection can lead to the discovery of functionally important genes. One possible aim is to discover genes that are relevant for the evolution of complex genetic and phenotypic traits. Recently, there has been a growing interest in identifying the genes that might be involved in population-level processes such as speciation and specialization. Both speciation and specialization genes are expected to evolve under positive selection. The possibility of comparing the genomes of species that have recently diverged is expected to facilitate the identification of genomic regions under selection and brings about the possibility of testing different speciation and specialization scenarios. We took such an approach using Microbotryum violaceum, a complex fungal sibling species, pathogen of different plant species of the Caryophyllaceae plant family. We have constructed a database of ESTs from cDNA libraries of four different Microbotryum species of putative nuclear genes expressed during conjugation and hyphal production, thus enabling us to identify genes involved in speciation and specialization. The public database MICROBASE provides access to all the sequences, assembled contigs and annotations for these genomes. We have compared the orthologs among the four species looking for genes under positive selection, particularly those involved in specialization and speciation traits.

08-02 Poster

MICROSATELLITE EVOLUTION REVEALED THROUGH GERM LINE MUTATIONS

Jarl A. Anmarkrud [1]

[1] *University of Oslo, Natural History Museum, P.O.box 1172, 0318, Oslo, Norway*

j.a.anmarkrud@nhm.uio.no

Background: Microsatellites are frequently used to assess a number of genetic approaches (e.g. molecular forensic, parentage testing, population genetics and phylogeny). These markers are expected to evolve neutrally and are thus considered to reflect genome-wide diversity. The mode of microsatellite evolution is not fully understood, except it is enforced by mutations. But the mechanisms and processes responsible for microsatellite variations are under insistent debate. Earlier studies of *de novo* mutations in avian species are based on fragment analyses (size patterns). Fragment analyses are not be able to detect interesting features such as substitutions, interrupting motifs and incidents of homoplasy.

Results: I will here present sequence data from a total of 32 germ line mutations in the polymorphic hypermutable microsatellite *HrU10* in barn swallow (*Hirundu rustica*) and tree swallow (*Tachycineta bicolor).* As expected, the mutation process involved is replication slippage.

Implications: The results give an insight of the complex structure in this microsatellite. *HrU10* is used for several pedigree analyses because of its polymorphism. Here we will demonstrate that *HrU10* has been subject for an intricate evolution which is reflected in the number of different interrupting motifs. The results also indicate that this microsatellite might not be suitable in pedigree analysis due to several occurrences of homoplasy.

08-03 Poster

PHENOTYPIC PLASTICITY IN THE MOUTH FORMS OF PRISTIONCHUS NEMATODES

Gilberto Bento [1], Ralf J. Sommer [1]

[1] *Max Planck Institute for Developmental Biology, IV - Evolutionary Biology, Spemannstr. 32-34, 72076, Tuebingen, Germany*

gilberto.bento@tuebingen.mpg.de

The aim of this research project is to study the evolutionary and ecological role of phenotypic plasticity, as well as its genetic basis. Nematodes of the genus *Pristiochus* show a variable ecology: they can be found as soil-dwelling animals or in necronimic association with scarab beetles. They show a dimorphism in their mouth form, where stenostomatous and eurystomatous worms have qualitative as well as quantitative differences. This dimorphism is thought to be of great ecological relevance since it underlies different feeding strategies. Using selection inbred lines we have shown that this dimorphism is a case of phenotypic plasticity. In addition, we are able to manipulate the reaction norm by changing the laboratory environment: starving the worms in their early larval development (until the J2 larval stage) causes a dramatic increase in the ratio of eurystomatous worms in all tested strains of *Pristionchus pacificus*. Interestingly, there is genetic diversity for the reaction norm between strains of *Pristiochus pacificus* and between different species of the genus *Pristionchus*. We are currently investigating the genetic (proximate) and evolutionary (ultimate) causes of the mouth dimorphism. The analysis of Recombinant inbred lines (RILs) indicates that a small number of loci are responsible for the differences in the developmental switch mechanism between the *P. pacificus* strains used in the generation of the RILs. Furthermore, we have also generated mutant lines where the reaction norm changes towards an increase in the ratio of stenostomatous worms. Mapping is ongoing in both the RILs and the mutant lines.

08-04 Poster

THE ROLE OF PREDATOR'S RISK OF INJURY IN PREDATOR-PREY INTERACTIONS

Oded Berger-Tal [1], Shomen Mukherjee [1], Burt P. Kotler [1]

[1] *Jacob Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Mitrani Dept. of Desert Ecology, 84990, Midreshet Ben-Gurion, Israel*

bergerod@bgu.ac.il

Interactions of predators and prey often constitute foraging games in which the values of the strategies of foraging prey individuals often depend on those of their predators, and vice versa. As such, understanding the predator's behavior is crucial. While foraging, predators can alter their time allocation and level of daring (willingness to risk injury), and they should do so according to their need for energy. Overall, predators should treat the risk of injury as part of a foraging cost. Furthermore, predators should allocate more time and be more daring when they are in greater need of energy. On the other hand, when they are well fed, they should be less willing to risk injury and therefore use safer tactics.

I investigated the role of risk of injury in the foraging decisions of the red fox, *Vulpes vulpes*, and the effects of the predator's state on its time allocation and daring. To do so, I presented 3 red foxes with paired food patches that differed only in the perceived risk of injury that incurred while exploiting them. I also manipulated the state of the foxes by offering supplemental food or by withholding food for up to 48 hours. I quantified fox foraging behavior by measuring their giving up densities of food (GUDs) left behind in the food patches. Despite variation in behavior among the foxes, all of them showed highly significant effects of both energetic state and riskiness of the patch on the amount of food they left in the patches. In particular, they left risky patches at higher GUDs and left higher GUDs in both patch types when in better energetic state. Thus, red fox treat the risk of injury as part of a foraging cost. Furthermore, they vary their degree of time allocation and daring according to their state. These results suggest that predators may be able manage fear in their prey. This variation of the predator behavior can be of utmost importance to our understanding of predator prey interactions.

08-05 Poster

PREDICTABLE VARIATION IN FORAGING BEHAVIOUR BASED ON BILL MORPHOLOGY IN DARWIN'S TREE FINCHES (CAMARHYNCHUS SPP.)

Rebekah A. Christensen [1], Sonia M. Kleindorfer [1]

[1] *Flinders University, School of Biological Sciences, GPO Box 2100, 5001, Adelaide, Australia*

christensen.rebekah@flinders.edu.au

We observed foraging behaviour of Darwin's small, medium, and large tree finches (Camarhynchus parvulus, C. pauper, and C. psittacula respectively) on one island of the Galapagos archipelago, across two years. We found differences in diet between the three species, with the small tree finch having the broadest diet. Significant differences were observed in foraging technique and substrate use between the three species, and these differences align with the respective bill morphologies of each species. Some variation in foraging behaviour between years was noted, and importantly in all three species, time to successful capture of a food item was longer in a drought year than in a year with normal rainfall. Our study is the first to provide a detailed analysis of foraging behaviour in Darwin's tree finches, and suggests that niche partitioning in Darwin's tree finches is based upon substrate use.

08-06 Poster

EVOLUTION OF EMBIOPTERA (WEBSPINNER INSECTS) SILK: COMPARATIVE ANALYSES OF SEQUENCE AND MECHANICAL PERFORMANCE

Matthew A. Collin [1], Cheryl Y. Hayashi [1]

[1] *University of California, Riverside, Department of Biology, University of California, 92521, Riverside, CA, United States*

mcoll002@student.ucr.edu

Silk production has independently evolved in several arthropod lineages, such as Acari, Araneae, Hemiptera, and Lepidoptera. Silk fibers are largely composed of proteins (fibroins) and unlike most other proteins, fibroins are used completely outside an organism's body. For many arthropods, silk fibers perform essential ecological functions that include protection, reproduction, dispersal and prey capture. The tight interaction between silk and organismal fitness enables selection on mechanical performance of fibroins. While moth and spider silks have been well studied, very little is known about the silks of other arthropods. One order, Embioptera (webspinners), is exceptional among silk-producing insects because they use silk throughout their lifetime rather than just for larval feeding and/or pupation. Webspinners spin sheet-like ribbons of silk from clusters of silk secreting glands in their forelimb tarsi. The primary function of this silk is to construct a network of protective tubes in which the embiopterans develop, forage, and reproduce. We constructed cDNA libraries from divergent webspinner species to determine their silk coding sequences. We found that the inferred webspinner fibroins are similar in amino acid composition and repetitive architecture to other arthropod silks, yet there are striking differences in the proportions of the amino acids and sequence details. By comparing the fibroin sequences and mechanical properties of webspinner silk to that of other arthropod silks, we will better understand the evolution of these ecologically important molecules.

08-07 Poster

RANGE-WIDE PATTERNS OF GENETIC DIVERSITY IN A NEOTROPICAL FOREST SPECIES, VRIESEA GIGANTEA (BROMELIACEAE)

C. Palma-Silva [1], G. M. Paggi [1], F. Bered [1], T. Barbara [2], C. Lexer [2], M. H. Bodanese-Zanettini [1]

[1] *Universidade Federal do Rio Grande do Sul, Laboratorio de Genetica Vegetal, IB, Porto Alegre, RS, Brazil*
[2] *Royal Botanic Gardens, Jodrell Laboratory, Kew, Richmond, Surrey, TW9 3DS, UK*

clarissepalma@yahoo.com.br

The role of climatic fluctuations of the Pleistocene on the distribution and genetic diversity of Neotropical species is largely unknown, in contrast to the knowledge on the evolutionary history of European and North American taxa. We report a species-wide survey of nuclear microsatellite genetic diversity in a plant endemic to the Atlantic Rainforest of Brazil: *Vriesea gigantea* Gaud (Bromeliaceae). Our goal is to initiate comparisons between patterns of species diversity and genetic diversity in this biodiversity 'hotspot'. Our results on patterns of genetic diversity are consistent with historical expansion from the Northern half of the present distribution range. The pattern of genetic differentiation among populations shows a geographic trend of decreasing genetic diversity from North to South. The center of genetic diversity described here for *V. gigantea* (states of Sao Paulo and Rio de Janeiro) is coupled with the center of species diversity and center of endemism for most animal and plant species of the Atlantic Rainforest. Our results clearly demonstrate that patterns of genetic diversity and species diversity of tropical and subtropical taxa are connected and possibly were shaped by the same historical forces: historical climatic changes of the late quaternary. Besides the geographic trend S-N, our analyses identified two geographical isolation barriers likely to be responsible for the separation of populations into geographic regions: South, Centre, and North. Moreover, restricted gene flow between populations has given rise to an isolation-by-distance pattern of differentiation with significant divergence among populations ($F_{ST} = 0.214$). The *within*-population inbreeding coefficient was significantly positive ($F_{IS} = +0.261$), and these heterozygote deficits stem from a combination of inbreeding and genetic subdivision. The conservation implications of the observed patterns of variability will be discussed.

08-08 Poster

GEOGRAPHIC STRUCTURE OF X-CHROMOSOME DRIVE IN DROSOPHILA NEOTESTACEA

Kelly A. Dyer [1]

[1] *University of Edinburgh, Institute of Evolutionary Biology, Ashworth Labs, W. Mains Rd,, EH9 3JT, Edinburgh, United Kingdom*

kelly.dyer@ed.ac.uk

Ecological factors can affect the evolutionary outcomes of selfish genetic systems, even when they otherwise enjoy a large selective advantage. In males carrying a driving X (X^D) chromosome, Y-bearing sperm fail to develop and thus the male sires only daughters. As a result of this meiotic drive, an X^D enhances its own transmission and may increase to a high frequency in a population (and potentially cause extinction due to a lack of males) even if it adversely affects the fitness of its carriers. However, restrictive ecological conditions and the evolution of suppressors on the autosomes and Y chromosome may limit or prevent the spread of an X^D. I am using the X-drive system in *Drosophila neotestacea*, thought to be a relatively young drive system, to explore how genetic and ecological factors affect variation in X^D frequency within and among populations. The geographic range of this mushroom-feeding fly extends throughout the temperate and boreal forests of North America, and among populations spanning this range I found that the frequency of the X^D varies tremendously, ranging from near absence to almost 30%. I will explore the factors that may directly or indirectly underlie this variation, including host population structure, the evolution of suppressors, and various ecological variables such as climate and population density. I will show that specific local ecological conditions rather than suppressors or restricted gene flow appear to underlie the distribution of the X^D in *D. neotestacea*, and suggest how these ecological factors may affect the evolution of selfish elements.

08-09 Poster

THE SIGNATURE OF SPECIATION IN ECOLOGICAL PATTERNS

Rampal S. Etienne [1]

[1] *University of Groningen, Community and Conservation Ecology Group, Box 14, 9750 AA, Haren, The Netherlands*

r.s.etienne@rug.nl

Our knowledge of speciation has been mostly fueled by the fossil record. However, there is an obvious limit to this record. Therefore, we should also find different ways of evidence for modes of speciation. I examine whether we can make inferences on speciation from (macro)ecological patterns such as species-abundance distributions and species-body-size distributions, using theoretical models of speciation in a community ecological context. Particularly I study the effect of the mode of speciation on species' abundances in a neutral context and the effect of body size on speciation in explaining the body size diversity distribution. I show that these effects can be profound, puzzling and/or counterintuitive.

08-10 Poster

PHYLOGENY AND COMPARATIVE ANALYSIS OF PLANT FUNCTIONAL TRAITS

Olivier Flores [1], Eric Garnier [1]

[1] *CEFE/CNRS, DSE, 1919, Route de Mende, 34293, Montpellier Cedex 5, France*

olivier.flores@cefe.cnrs.fr

The comparative approach seeks to establish fundamental rules that explain trait variability at the individual, population and species levels, with a particular emphasis on invariants and/or tradeoffs and constraints on how organisms function. This approach allows for a rigorous extrapolation and prediction of species response. One of our objectives here is to synthesize information in existing data bases of plant functional traits and conduct comparative analyses at the species/population levels in order to assess general mechanisms.

Trait variability corresponding to major functions are explored in relation with two principal determinants of species distributions, *i.e.* disturbance regime and resource availability. This approach leads to a precise predictive capacity of species replacement along environmental gradients. Phylogenetic information will be incorporated to integrate dependence among trait values due to phylogenetic history, *i.e.* to disentangle trait variations associated with a common evolutionary history from those that represent cases of convergent evolution.

We particularly investigate the influence of phylogeny on the present-day distributions of several leaf traits (dry matter content, specific leaf area, leaf nitrogen) through different methods. Major divergences across clades and their contribution to those distributions are quantified in order to trace a possible phylogenetic signal and the evolution of those traits.

08-11 Poster

EVOLUTION OF THE GUSTATORY AND OLFACTORY RECEPTOR GENE FAMILIES WITHIN THE GENUS DROSOPHILA; THE INFLUENCE OF SELECTION, SPECIALISATION AND GENOME SIZE

Anastasia Gardiner [1], Daniel Baker [1], Roger Butlin [2], William Jordan [3], Mike Ritchie [1]

[1] *St. Andrews University, Biology, Dyers Brae House, KY169TH, St. Andrews, Fife, Scotland, UK*
[2] *University of Sheffield, Animal and Plant Sciences, Western Bank, S10 2TN, Sheffield, England, UK*
[3] *Institute of Zoology, Regent's Park, NW1 4RY, London, UK*

ag91@st-andrews.ac.uk

Insect's behaviours are driven by chemoreception, chemical cues are recognized by large families of olfactory and gustatory receptors (Or and Gr). Comparison of the Or/Gr families of the fruit fly, mosquito and honey bee shows very strong interspecific divergence associated with individual species' adaptations and responses to their environment. We have identified the Ors and Grs in recently sequenced *Drosophila* species, including generalist, specialist and endemic species. We found that both (Or and Gr) gene families have evolved through gene duplication, pseudogenisation and gene loss. The observed sequence diversity implies a predominant history of purifying selection with diversifying selection influencing a small fraction of loci. Accelerated expansion of copy number for several Or and Gr genes was observed in *D. ananassae, D. willistoni* and *D. grimshawi*. The changes we have described amongst twelve species show how the families have changed during species divergence, and aspects of this evolution might reflect species' adaptation to their chemical environment, though the best predictor of the extent of gene duplication is total genome size. We find a significant effect of endemism rather than specialisation on the proportion of pseudogenes. It is likely that endemism will lead to relaxed selection followed by selective expansion of particular loci during colonisation, and perhaps an overall increase in genome size so these factors are probably interrelated.

08-12 Poster

USING DNA METHYLATION PATTERNS TO INVESTIGATE THE DYNAMICS OF EPIGENETIC DIVERSITY AMONG CELLS AND AMONG INDIVIDUALS

Diane P. Genereux [1]

[1] *University of Washington, Department of Biology, Seattle WA, USA*

genereux@u.washington.edu

Both eukaryotic and prokaryotic organisms use DNA methylation to encode epigenetic information. DNA methylation regulates gene expression, and thus can produce phenotypic differences among cells and among individuals, even in the absence of genetic mutations. Altered DNA methylation patterns are characteristic of several human diseases, including some breast and colon cancers. These results suggest that preservation of epigenetic information over multiple rounds of DNA replication is crucial for moderating the risk of epigenetic diseaese. However, recent examples from mammals suggest that the imperfect fidelity of epigenetic information transmission may be required for DNA methylation to encode information about environmental conditions. Have observed eukaryotic epimutation rates evolved as a tradeoff between maintaining existing information, and encoding new environmental signals? To

begin to address this question, we have developed molecular and mathematical methods to estimate the fidelity of epigenetic information in eukaryotic genomes. Hairpin-bisulfite PCR provides information on the detailed methylation patterns on both strands of individual, double-stranded DNA molecules, yielding snapshots of molecular phylogenetic history; we developed a mathematical model to estimate epigenetic fidelities from these double-stranded patterns. Here, I will discuss our current work to investigate potential conflicts between genetic and epigenetic fidelities in somatic tissues, and will describe our molecular and mathematical approaches to investigate the cellular population dynamics of epigenetic fidelity and flexibility in Linnaeus's peloric "monster flower", recently disocvered by Cubas et al. to be an epimutant

08-13 Poster

COMPARATIVE PHYLOGEOGRAPHY OF BOREAL FOREST SPECIES IN NORTHERN EURASIA

Vadim B. Fedorov [1], Anna V. Goropashnaya [1]

[1] *UAF, Institute of Arctic Biology, 902 Koyukuk Drive, 99775, Fairbanks, Alaska, United States*

fnag@uaf.edu

In order to infer refugial and colonization history, we studied association between genealogy and geographic distribution of the mtDNA cytochrome *b* haplotypes, and demographic history in the wood lemming, species obligatory associated with the boreal forest, across the Eurasian taiga zone from Scandinavia to the Pacific coast. To reveal general trends in biotic history of the taiga zone, we compared phylogeographic structure and demographic history of the wood lemming with published patterns of genetic variation in other boreal forest species studied to date across Eurasia: the flying squirrel, Siberian newt, red wood ants, great and willow tits, great-spotted and three-toed woodpeckers. Comparison of phylogeographic structure across taxonomically diverse array of species ecologically associated with the taiga forest revealed similar pattern with the two general aspects. First, the major south - north phylogeographic discontinuity observed in the five out of six species studied in the south eastern Siberia and Far East implies vicariant separation in two different refugial areas. Limited distribution range of the south eastern lineages gives no evidence for the importance of the putative south eastern refugial area for postglacial colonization of northern Eurasia by boreal forest species. Second, the lack of phylogeographic divisions associated with significant reciprocal monophyly, and genetic signs of demographic expansion in all nine boreal forest animal species studied to date across most of northern Eurasia imply contraction of each species to a single refugial area during the late Pleistocene followed by range expansion on a continental scale. The time estimates of demographic expansion in total of the four species of insects and mammals are compatible with the period of forest advances during the last interglacial. The similar phylogeographic pattern observed in the taxonomically diverse set of organisms with different life histories and dispersal potentials suggests that this similarity reflects historical dynamics of their common environment, the taiga forest in northern Eurasia.

08-14 Poster

EFFECTS OF MIGRATION ON THE GENETIC COVARIANCE MATRIX

Frédéric Guillaume [1], Michael C. Whitlock [1]

[1] *University of British Columbia, Department of Zoology, #2370-6270 University Blvd., V6K 1Z4, Vancouver, BC, Canada*

guillaum@zoology.ubc.ca

In 1996, Schluter showed that the direction of morphological divergence of closely related species is biased toward the line of least genetic resistance, represented by gmax, the leading eigenvector of the matrix of genetic variance-covariance (the G-matrix). G is used to predict the direction of evolutionary change in natural populations. However, this usage requires that G is sufficiently constant over time in order to have enough predictive significance. Here, we explore the alternative explanation that G can evolve due to gene flow to conform to the direction of divergence between incipient species. We use computer simulations in a mainland-island migration model with stabilizing selection on two quantitative traits. We show that a high level of gene flow from a mainland population is required to significantly affect the orientation of the G-matrix in an island population. The changes caused by the introgression of the mainland alleles into the island population affect all aspects of the shape of G (size, eccentricity, and orientation) and lead to the alignment of gmax with the line of divergence between the two populations' phenotypic optima. Those changes decrease with increased correlation in mutational effects and with correlated selection. Our results suggest that, high migration rates, such as those often seen at the intra-specific level, will substantially affect the shape and orientation of G, whereas low migration (e.g., at the inter-specific level) is unlikely to substantially affect the evolution of G.

08-15 Poster

SPATIAL STRUCTURE INHIBITS THE RATE OF INVASION OF BENEFICIAL MUTATIONS IN ASEXUAL POPULATIONS

Michelle G. J. L. Habets [1], Tamás Czárán [2], Rolf F. Hoekstra [1], J. Arjan G. M. De Visser [1]

[1] Wageningen University, Laboratory of Genetics, Arboretumlaan 4, 6704 BD, Wageningen, The Netherlands
[2] Hungarian Academy of Sciences and Eotvos Lorand University, Theoretical Biology and Ecology Research group, Pázmany Péter sétány 1/C, H-1117, Budapest, Hungary

michelle.habets@wur.nl

Populations in spatially structured environments may be divided into a number of (semi-) isolated subpopulations due to limited offspring dispersal. Limited dispersal and, as a consequence, local competition could slow down the invasion of fitter mutants, allowing short-term coexistence of ancestral genotypes and mutants. We determined the rate of invasion of beneficial mutants of *Escherichia coli,* dispersed to different degrees in a spatially structured environment during 40 generations, experimentally and theoretically. Simulations as well as experimental data show a decrease in the rate of invasion with increasingly constrained dispersal. When a beneficial mutant invades from a single spot, competition with the ancestral genotype takes place *only* along the edges of the growing colony patch. As the colony grows, the fitness of the mutant will decrease due to a decrease in the mutant's fraction that effectively competes with the surrounding ancestor. This prevents the beneficial mutant from rapidly invading, despite its inherently higher competitive ability. Because inferior competitors are present in the community for a longer period of time, we expect not only the ecology, but also the evolution of the community to be influenced; higher standing genetic variation may facilitate populations to adapt to changing environments. In addition, it may provide more opportunities for stable coexistence between certain genotypes. Thus we arrive at the conjecture that by slowing down the exclusion dynamics between competing genotypes, spatial constraints may increase evolutionary diversification of populations.

08-16 Poster

ECOLOGICAL SEGREGATION OF SYMPATRIC FISH SPECIES: DEPTH OF OCCURRENCE, NOT SPECIES IDENTITY, DETERMINES DIET COMPOSITION

Ingeborg P. Helland [1], Chris Harrod [2], Jörg Freyhof [1], Thomas Mehner [1]

[1] Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Biology & Ecology of Fishes, Müggelseedamm 310, 12587, Berlin, Germany
[2] Queen's University Belfast, School of Biological Sciences, Medical Biology Centre, 97 Lisburn Road, BT9 7BL, Belfast, UK

helland@igb-berlin.de

In the deep, oligotrophic lake Stechlinsee (North-Germany) two recently diverged fish species, the European winter-spawning vendace *Coregonus albula,* and the endemic dwarf-sized spring-spawning Fontane cisco *Coregonus fontanae*, co-occur. The two species show morphological as well as genetical differences, and are considered candidates for postglacial sympatric speciation. However, to date, ecological and life-history differences between the species have not been well explored, although they are considered to be key factors in sympatric speciation. It has been shown that the majority of both populations exhibit diel vertical migrations (DVM) between deep hypolimnetic zones and layers close to the thermocline. Habitat differentiation between the species appears to be limited and both exploit the food resources in the pelagic area. However, it was hypothesised that the species pair differs in diet composition, which might have contributed to their divergence. By combining gut analyses (GCA) and stable isotope analyses (SIA) we compared the diet of the two species from samplings at different depths over ten months. Overall, SIA and GCA both showed surprisingly little trophic differences between the two species, but a significant effect of depth on individual diet. Thus, it seems that the sympatric species pair in Stechlinsee does not follow the expected pattern of niche segregation along the limnetic-benthic axis typical of other postglacial sympatric fish species pairs.

08-17 Poster

EFFECTS OF PAST AND PRESENT CONDITIONS ON LIFE HISTORY TRAITS IN THE BANK VOLE

Heikki Helle [1], Esa Koskela [1], Tapio Mappes [1]

[1] *University of Jyväskylä, Dept. of Biological and Environmental Science, P.O. Box 35, 40014, Jyväskylä, Finland*

heihell@jyu.fi

The effects of present environmental conditions on life history strategies have been thoroughly studied, but the effects of growing conditions should also be considered when exploring life history traits and their trade-offs. Replicated experimental studies on long-term effects of the growing environment in wild mammals are still lacking. In this study, we examine the effects of past and present environmental conditions on reproduction and survival in the bank vole (*Myodes glareolus*). The experiment was carried out during a summer and following winter in 16 outdoor enclosures. Good-quality conditions were created by supplementary feeding whereas non-supplemented enclosures served as controls (poor-quality conditions). The early development of bank voles took place during the summer in either good-quality or control conditions. After summer, the treatment of half of the individuals was changed, while the other half continued with the same treatment. The results showed that in females, neither the past nor present conditions affected their survival significantly, whereas in males, good growing conditions lowered male survival over winter. In females, good over-wintering conditions increased the probability of breeding and advanced the initiation of breeding. However, conditions during early development significantly affected the characteristics of litters: females growing in good-quality conditions produced larger litters with bigger pups and a male-biased sex ratio. The results reveal that in addition to the present environment, the conditions experienced early in life also affect life history traits and should be recognised when assessing the fitness of an individual.

08-18 Poster

LATITUDINAL VARIATION IN SEXUAL SIZE DIMORPHISM IN A WIDESPREAD AMPHIBIAN

Dragana Cvetković [1], Vladimir Jovanović [1]

[1] *University of Belgrade, Faculty of Biology, Studentski trg 16, 11000, Belgrade, Serbia*

dragana@bf.bio.bg.ac.yu

Large-scale patterns of body size variation and sexual size dimorphism (SSD) have attracted much research interest; these patterns are described by well known generalizations such as Bergmann's and Rensch's rule. Allometry for SSD, common in many groups of animals and plants, is studied not only at interspecific level, but among conspecific populations as well.In this study, we used published data of sex-specific body size variation in common toad (*Bufo bufo*), anuran species with wide distribution in Europe. Fifteen analysed populations represented broad latitudinal range, from 42°N (Montenegro) to 63°N (Norway). The aim was to explore if there was systematic variation in sexual size dimorphism with latitude and to investigate whether the patterns among conspecific populations were equivalent to Rensch's rule. A pattern of allometry for sexual size dimorphism that conforms to Rensch's rule emerges when male size is more variable than female size. In our study, male and female body sizes exhibited typical high positive correlation (r=0.945); however, female size varied more than male size. The slope of reduced major axis regression of log (male size) on log (female size) deviated from 1.0; values greater than 1.0 generally indicate patterns equivalent to Rensch's rule. However, in our sample the slope was significantly lower than 1 ($p<0.01$). Female latitudinal body size cline was steeper than that of males, revealing the pattern inconsistent with a latitudinal variant of Rensch's rule.

08-19 Poster

SPATIAL AND TEMPORAL VARIATION OF SEX RATIO AND PLANT SIZE IN DIOECIOUS MERCURIALIS PERENNIS (EUPHORBIACEAE)

Vladimir Jovanović [1], Dragana Cvetković [1]

[1] *University of Belgrade, Faculty of Biology, Studentski trg 16, 11000, Belgrade, Serbia*

gvaihir@gmail.com

In sexually dimorphic plant species, spatial and temporal patterns of sex ratio variation, spatial segregation by gender along gradients and differential investment of the two sex functions have attracted much research interest. In dioecious plants, the resource investment in reproduction is typically greater for females than for males, and this may have sex specific consequences on growth rates and result in sexual size dimorphism. The aim of this study was to examine variation in sex ratio and plant size in populations of *Mercurialis perennis* L. (Euphorbiaceae), a dioecious anemophilous species with wide geographical and altitudinal distribution in Europe. Analysed populations from Serbia represented altitudinal range 196m – 1480m a.s.l. Interannual variation in analysed traits was examined in low altitude populations (<500m a.s.l.). Our study reveals significant variation in sex ratio among populations of *M. perennis* and supports the notion of spatial segregation of sexes along altitudinal gradient. Deviations from unity sex ratio were significant in all analysed populations except one; in majority of populations it was highly significant ($p<0.001$). The direction of bias changed with altitude – the frequency of males decreased with increasing altitude. Some previous studies suggested that, contrary to current hypothesis, females of herbaceous perennials are often the larger sex. In our study, however, the results on intersexual differences in plant height generally fit the hypothesis – males were the larger sex (though the difference was not significant in highest altitude population). The average plant size, as well as intersexual differences in this trait, decreased with increasing altitude.

08-20 Poster

EVOLUTIONARY ORIGINS OF WIDESPREAD SMALL BENTHIC CHARR (SALVELINUS ALPINUS) IN SMALL LACUSTRINE LOCATIONS IN ICELAND

Kalina H. Kapralova [1], Guðbjörg A. Ólafsdóttir [1], Sigurdur S. Snorrason [1], Michael Morrissey [2], Moira Ferguson [2]

[1] *University of Iceland, Biology, Grensasvegur 12, IS101, Reykjavik, Iceland*
[2] *University of Guelph, Integrative biology, 50 Stone road East, N1G 2W1, Guelph, Canada*

khk2@hi.is

The colonization of novel habitats is thought to be a potential trigger of speciation. In Iceland, small bentic morphospecies of Arctic charr *(Salvelinus alpinus)* occur widely in small lacustrine habitats. We tested two competing hypotheses regarding the origin of small benthic charr in Iceland. First the small benthic phenotype may have evolved multiple times in similar habitats. Under this hypothesis, natural selection and the environment play a pivotal and predictable role in phenotypic evolution and speciation. Alternatively, this phenotype may have evolved once or few times and is now widespread due to subsequent dispersal. The first hypothesis predicts that small benthic charr populations will be genetically most similar to nearby charr with other phenotypes. The second predicts that widespread populations of small benthic charr will be most similar to one onother. We collected genetic samples from 19 small benthic populations throughout Iceland, as well as from available reference populations of other forms of charr. Samples were genotyped at six microsatellite loci. Using several standard population genetic analyses, we evaluated predictions of our two competing hypotheses.

08-21 Poster

THE IMPLICATIONS OF HABITAT OVERLAP FOR THE STUDY OF HABITAT-MEDIATED SELECTION

Sophie Karrenberg [1], Adrien Favre [1]

[1] *ETH Zurich, Integrative Biology, Universitätstrasse 16, 8092, Zurich, Switzerland*

sophie.karrenberg@env.ethz.ch

Ecological differentiation is a major contributor to reproductive isolation. However, even when diverging or hybridizing lineages have different ecological requirements, substantial habitat overlap can still occur, as demonstrated here for two hybridizing species of Silene. We investigated habitat differentiation between the naturally hybridizing species pair Silene dioica and S. latifolia using AFLP phenotypes and corresponding vegetation relevées around individual plants. 19 study sites were distributed throughout the Swiss Alps and included pure populations and contact sites (both species present within 30 m). The two species show consistent differences in AFLP phenotypes in pure populations and habitat analysis revealed that S. dioica occurs in moister, colder and less disturbed sites that S. latifolia. However, it was also evident that the two species can share habitat conditions across sites. Contact sites were found at such intermediate conditions and within contact sites, strongly bimodal patterns of AFLP phenotypes were detected. Evidence for habitat-genotype associations within contact sites was weak making habitat-mediated selection against intermediate hybrids unlikely. Habitat overlap may substantiually influence conclusions from studies of habitat-mediated selection. We argue that the detection of habitat-mediated selection pressures on immigrants or hybrids depends less on the magnitude of the difference between the habitats compared than on the position in the continuum of differentiated and overlapping habitat conditions for the involved taxa. Habitat-mediated selection pressures and thus habitat-genotype associations are expected to be largest when differentiated habitats are compared, and smaller when habitats where both species can potentially occur are involved. Of course, this may be an (over-)simplification, as fitness may decline toward marginal habitats and local adaptation within species can complicate the picture. Nonetheless, detailed study of habitat parameters that can detect habitat overlap between taxa may help to refine the understanding habitat-mediated selection.

08-22 Poster

MICROEVOLUTIONARY AND ECOLOGICAL DIFFERENCES OF SELF-FERTILIZING PRISTIONCHUS PACIFICUS STRAINS WITH WORLDWIDE DISTRIBUTION

Simone Kienle [1], Hans Zauner [1], Ralf J. Sommer [1]

[1] *MPI for Developmental Biology, Dept. for Evolutionary Biology, Spemannstrasse 37, 72076, Tübingen, Germany*

simone.kienle@tuebingen.mpg.de

The ultimate understanding of evolutionary systems requires an integration of the population-based evolutionary theory with developmental biology and ecology. To this end, we combine studies in evolutionary developmental biology with microevolution and ecology by focussing on the nematode *Pristionchus pacificus*.

Recent field studies revealed not only a worldwide distribution of *Pristionchus*, but also a close association with scarab beetles. *P. pacificus* was found on the oriental beetle (*Exomala orientalis*) in Japan and the US. To obtain insight into the genetic variation of *P. pacificus* we investigated the molecular diversity of 21 nuclear markers with known position on the genetic linkage map for 48 isolates. In a total of 2871bp of nuclear DNA, located across all six chromosomes, we found 83 polymorphic sites. Levels of linkage disequilibrium are high within and also across chromosomes, indicating rare outcrossing. Analysis of 2 mitochondrial genes, ND6 and ND4L, in 71 isolates revealed substantial sub-structuring of the worldwide population. In particular, 38 strains collected in Japan group together. Additionally, 15 of the available *P. pacificus* isolates have been selected for detailed analysis of variations in life history traits and developmental processes. Temperature shift experiments (shift from 20 to 30°C) and gonad ablation experiments indicate a high degree of diversity between strains.

In conclusion, our microevolutionary studies in *P.pacificus* are in strong contrast to *Caenorhabditis elegans* , with respect to both, population structure and the type of developmental variability.

08-23 Poster

HIERARCHICAL ALLOCATION TO LIFE-HISTORY TRAITS IN A LIZARD WITH INVARIANT CLUTCH SIZE: GROW FIRST, BREED THEN, GET FAT FINALLY

Lukáš Kubička [1], Lukáš Kratochvíl [1]

[1] *Charles University, Department of Ecology, Viničná 7, 12844, Praha 2, Czech Republic*

kubicka@centrum.cz

Most reptile species possess undetermined growth and produce large clutches, where clutch size, but not egg size, correlates with female size. Females are believed to produce eggs of size optimal for a given population. Most phenotypically plastic life-history decisions made by individual females should then concern proportion of resources allocated to reproduction versus soma (growth, maintenance and storages), clutch frequency and clutch size. However, estimation of allocation to particular life-history traits in reptiles is usually complicated by low frequency of clutches. Gecko females produce maximally two eggs per clutch, but clutches are frequent. Therefore, geckos can serve as an excellent model for studying nutrition-dependent plasticity/canalization in resource allocation. Here, we report results of the laboratory experiment in females of the gecko species *Paroedura picta*. Small adult females chosen from outbred livestock were fed either by 0.5 gram of crickets per day or obtained 2/3 of this amount for 7 months. Females in both treatment groups followed the same growth trajectory in body length. On the other hand, allocation to reproduction was highly nutrition-dependent. Although all females produce eggs regularly, food-limited females laid smaller eggs and have larger interclutch intervals. As small eggs suffered higher mortality during incubation and there was a correlation between egg size and hatchlings' size, food-limited females compromised both quantity and quality of propagules. Fat storages were formed only in well-fed females, probably after reaching of their maximal reproductive output. We suggest that subsequent allocation to growth, reproduction and fat storage reflects meaningful strategy of investment, and discuss evolutionary consequences of hierarchical allocations.

08-24 Poster

SPECIATION ON THE HIGH ANTARCTIC SHELF – POPULATION GENETIC IMPLICATIONS FROM THE GIANT ISOPOD CERATOSEROLIS TRILOBITOIDES (EIGHTS, 1833)

Florian Leese [1], Christoph Held [1]

[1] *Alfred Wegener Institute for Polar and Marine Research, Marine Animal Ecology, P.O.Box 12 0161, D-27515, Bremerhaven, Germany*

florian.leese@awi.de

The Antarctic continental shelf is characterized by the lack of physical barriers on the shelf and strong circum-Antarctic current systems that should promote high gene flow between populations. However, recent work on cryptic species has shown that many Antarctic species previously believed to be widely distributed in fact consist of many, reproductively isolated species with much smaller, allopatric distribution patterns around the continent.

In view of the prevailing circumstances that make allopatric speciation less likely to occur, we have for the first time studied the population structure and gene flow patterns of a model species on the High Antarctic shelf - the giant isopod *Ceratoserolis trilobitoides* (Eights, 1833). Genotyping 442 specimens of 10 different populations using 12 newly developed microsatellite markers and 16S and COI mtDNA markers, we found moderate amounts of gene flow even between populations isolated by about 3000 kilometres. Gene flow patterns, however, deviate from a simple 'isolation by distance' model being almost unidirectional. Source populations are located in the Eastern Weddell Sea and sink populations around the Antarctic Peninsula.

The asymmetry in gene flow is likely to be a result of the current regime in the Weddell Sea (Weddell Gyre). Currently, a scenario of recurrent glaciations of major parts of the Antarctic continental shelf and lineage sorting within ice-free refugia during glacial maxima appears to be in best accordance with our data and biogeographical findings.

08-25 Poster

EXPERIMENTAL EVOLUTION OF RESISTANCE TO NEMATICIDES IN C. ELEGANS

Patricia S. C. Lopes [1], Henrique N. P. Teotónio [1], Elio Sucena [1], Sara N. R. Magalhães [1]

[1] *Instituto Gulbenkian da Ciencia, Evolutionary Genetics, Rua da Quinta Grande, 6, 2780-156, Oeiras, Portugal*

plopes@igc.gulbenkian.pt

Most studies on pesticide resistance in natural populations or in strains produced by mutagenesis have shown that resistance is obtained by one or a few mutations in the binding site of the pesticide. This suggests that there are intrinsic limits to the resistance mechanisms expressed. To verify whether this is the case, the evolution of resistance should be tackled under the defined and reproducible conditions typical of experimental evolution designs.

The genetic basis of resistance to the nematicide ivermectin in *Caenorhabditis elegans* was described for mutagenized strains as the synergistic action of mutations located mainly on 3 genes. We tested whether the same mechanism of resistance was obtained in lines of experimental evolution in the laboratory. In each generation, nematodes were exposed to a concentration of ivermectin resulting in 90% mortality in the initial population. The evolution of resistance was assessed by measuring population size every generation. A sample of individuals was frozen every 3 generations. Once resistance was widespread, we tested whether mutations in the candidate genes had occurred at each stage of the evolutionary process, including in the original base population. In addition, we measured the evolution of phenotypic traits associated to adaptation to novel environments, namely fecundity and survival in the environment with the nematicides. Furthermore, a cost of resistance was assessed by comparing trait values in the ancestral environment between resistant and susceptible populations.

Our results will measure how reproducible are genetic changes during the evolution of pesticide resistance, and this will contribute to our knowledge of the repeatability of adaptation processes.

08-26 Poster

PLANTS WITH BODY GUARDS INVEST LESS ON MECHANICAL AND CHEMICAL DEFENCES

Ana L. Llandres [1], Miguel A. Rodríguez-Gironés [1], Rodolfo Dirzo [2]

[1] *Estación Experimental de Zonas Áridas. CSIC, Departamento de Ecología Funcional y Evolutiva, C/ General Segura Nº1, 04001, Almería, Spain*
[2] *Stanford University, Department of Biological Sciences, 385 Serra Mall, 94305, Stanford, California*

allandres@eeza.csic.es

Plants have evolved several anti-herbivory strategies, ranging from chemical and mechanical defences, to the recruitment of mutualistic defenders ("body guards"), invertebrates (ants, wasps) that prey on phytophagous insects. In order to examine whether investment on mechanical and chemical defences differs between plants with and without body guards, we compared the standing herbivory and palatability of congeneric species with (*Cordia alliodora* and *Croton suberosus*) and without (*Cordia elaeagnoides* and *Croton pseudoniveus*) body guards at two ontogenetic stages: before and after the recruitment of body guards. Species with body guards were more palatable than species without them, a result that was obtained for the adult and juvenile stages in both genera. In species with body guards as adults, juveniles were less palatable than adults, but this was not the case in species without body guards. Despite these differences in palatability, species with body guards suffered less herbivory than species without them. We conclude that body guards are an effective defence against herbivores and that their recruitment allows plants to reduce investment on other defence mechanisms, supporting the notion of a tradeoff among defensive mechanisms.

08-27 Poster

IS THERE A TREND IN BIOLOGICAL COMPLEXITY: A PHYLOGENETICAL APPROACH ?

Nicolas Maughan [1], Pierre Pontarotti [2]

[1] *Université de Provence, case 18, AEEB, Biodiversity & Environment Laboratory, 3 place Victor Hugo, 13331, Marseille, France*
[2] *Université de Provence, case 19, AEEB, Evolutionary Biology Laboratory, 3 place Victor Hugo, 13331, Marseille, France*

nicolas.maughan@up.univ-mrs.fr

Complexity is one of those problematic terms that has been used to describe so many objects and phenomena as to have lost any generally recognized precision or meaning. Many works tried to show an increase in metazoans complexity through time. In describing organisms, two of the most common usages are in reference to the number of different cell types or number or functional specialization of parts. For example, authors suggested several distinct categories of complexity (including the case of cell-type number) can be used to describe compositions and processes at different levels of biological organization, from molecular to ecological organization. If we consider the number of different cell types in a phylum, this one can refer to one categories of the complexity which would be a function of the number of different physical parts in a system. This criteria of complexity has been widely used in the litterature. However, it has been used by comparing different present-day species. For example, comparison of the cell-type number between lophotrochozoans and vertebrates. With such analyze one could state that a mouse, for example, is more complex than a worm. But, this doesn't indicate that the number of cell types increases in the mouse lineage. Moreover, paleontological data (fossils) give few indications to determine number and history of the ancestral cell-type. We therefore need a phylogenetical approach to know if the number of cell types increases in a phylum. Our communication will be drawn towards two points. First, we will study if the use of different cell-type is really relevant to evaluate complexity between organisms. Secondly, we will try to define which kind of reconstruction methods, for example parsimony or maximum likelihood, could be interesting to determine the number of different cell types (and an emergence order if it's possible) in the ancestral states in a specific phylum.

08-28 Poster

GEOGRAPHIC VARIATION IN CHILEAN POPULATIONS OF BUFO SPINULOSUS (ANURA: BUFONIDAE): INTERPRETING THE RELATIVE CONTRIBUTION OF PROXIMATE AND ULTIMATE FACTORS IN ADULTS AND LARVAE MORPHOLOGY AND LIFE HISTORY TRAITS

M. Méndez [1], E. R. Soto [2], M. Sallaberry [2], L. Pastenes [1], C. Correa [1], P. Jiménez [2], L. F. Hinojosa [3], P. Iturra [4]

[1] *Universidad de Chile, Laboratorio de Genómica Evolutiva, INTA, Macul 5540, PO Box 138-11, Santiago, Chile*
[2] *Universidad de Chile, Laboratorio de Vertebrados, Las Palmeras 3425, PO Box 653, Santiago, Chile*
[3] *Universidad de Chile, Facultad de Ciencias, Las Palmeras 3425, PO Box 653, Santiago, Chile*
[4] *Universidad de Chile, ICBM, Facultad de Medicina, Avda. Independencia 1027, Santiago, Chile*

mmendez@inta.cl

In Chile B. spinulosus has an extended geographic distribution (18ºS to 33ºS), from sea level to 4600 m. We studied the morphological and life history traits variation in larvae and adults from three populations of Northern Chile and two of Central Chile. We examined the potential influence of maternal effect, genetic differentiation (cytochrome b and control region mitochondrial genes) and abiotic factors (pH, temperature, oxygen, latitude, altitude, precipitation level) in the attributes variation. Our results showed that female size determinate both eggs number and egg size, and that there is no effect of locality, altitude or latitude. PCA and Discriminant Analysis (DA) in larvae and adults morphology showed significant differences among localities, being more pronounced in larvae (all localities are different by DA) than adults where some populations showed differentiation by DA. In contrast, the genetic study showed a lower level of differentiation among populations, especially those from Northern Chile, suggesting that the morphological divergence could be mainly produced by phenotypic plasticity. Finally, the Redundancy Analysis showed that in the larvae the morphometric variation is mainly correlated by a combination of pH and oxygen levels, while in adults the relevant factors are latitude, altitude and rainfall. Interestingly, the genetic differentiation was not a relevant factor that contributed to explain the morphological variation.

08-29 Poster

UV DEPRIVATION AFFECTS SHOALING PREFERENCES IN THREE-SPINED STICKLEBACKS

Ricarda Modarressie [1], Christian Günther [1], Theo C. M. Bakker [1]

[1] *University of Bonn, Institute for Evolutionary Biology and Ecology, An der Immenburg 1, 53121, Bonn, Germany*

rmodarressie@evolution.uni-bonn.de

Shoaling behaviour in fish is influenced by numerous factors, such as familiarity, group size and shoal composition. Grouping decisions are based on both olfactory and visual cues. The visual system of many vertebrates is extended into the UV waverange as in the three-spined stickleback (*Gasterosteus aculeatus*). Three-spined sticklebacks also possess UV-reflective regions on their body surface and prefer to shoal with shoals seen under full-spectrum light over shoals under light lacking UV.

In the present study, we tested the influence of different lighting regimes during rearing on shoaling behaviour. To that aim, one half of sibling groups were raised under full-spectrum lighting conditions (UV+: 300-700nm), and the other half under lighting conditions lacking the UV waverange (UV-: 400-700nm). We tested shoaling preferences in a binary choice set-up. Testfish, either from UV+ or UV- rearing groups, could simultaneously choose between a shoal seen through a UV-transmitting optical filter and another shoal behind a UV-blocking optical filter. Shoaling behaviour of testfish from the UV- rearing groups differed significantly from UV+ testfish. UV- testfish associated significantly longer with the shoal that could be seen through the UV-blocking (UV-) optical filter. Testfish from the UV+ rearing group showed no significant preference. The results suggest, that lighting conditions during rearing affect shoaling behaviour in sticklebacks.

08-30 Poster

FECUNDITY SELECTION ON THE GENETICAL COMPONENT OF JUVENILE GROWTH RATE VARIATION IN A STREAM-DWELLING SALMONID FISH, THE BROOK CHARR SALVELINUS FONTINALIS, IN FRESHWATER RIVER, CAPE RACE, NEWFOUNDLAND

Michael B. Morrissey [1], Moira M. Ferguson [1]

[1] *University of Guelph, Department of Integrative Biology, Department of Integrative Biology, University of Guelph, N1G 2W1, Guelph, Ontario, Canada*

mmorriss@uoguelph.ca

Natural selection is often described statistically as covariance between phenotype and fitness. In fact, natural selection is an evolutionary force only when fitness covaries with genetically-based phenotypic differences among individuals. In brook charr (*Salvelinus fontinalis*) in Freshwater River, a positive phenotype-fitness relationship has been reported for juvenile body size. However, juvenile body size in this river is among the smallest in the species. We tested the hypothesis that the selective regime with respect to reproductive success and the genetic component of juvenile body size is consistent with the small body size that is observed in this population. We used molecular parentage assignment and quantitative genetic principles to calculate indicies of the genetic potential for offspring body size of mature individuals. We then regressed estimates of reproductive success on these indicies. We evaluated the predictions that this regression would be weak (small or insignificant slope), negative, and/or indicative of disruptive or stabilizing selection.

08-31 Poster

PENDULUM PHYSICS EXPLAINS THE EVOLUTION OF SPIDER MORPHOLOGY

Jordi Moya-Laraño [1], Dejan Viković [2], Guadalupe Corcobado [1], Eva De Mas [1, 3], Eulaila Moreno [1]

[1] Estación Experimental de Zonas Áridas, CSIC, Ecología Funcional Y Evolutiva, General Segura, 1, 04001, Almería, Spain
[2] Institute for Advanced Study, Program for Interdisciplinary Studies, Einstein Drive, 08540, Princeton, NJ, USA
[3] Universitat de Barcelona, Biologia Animal, Avda. Diagonal, 645, 08028, Barcelona, Spain

jordi@eeza.csic.es

The morphological adaptations and constraints of moving upside-down are not well understood. An animal that has to move in this position is less constrained in how long or thick its legs can be relative to a normally-walking animal. This is because animals that stand on their legs function as an inverted pendulum, in that at each step they have to lift a large proportion of their body mass. Thus, relatively wider legs are required for ensuring enough muscle power for walking and running. Hanging animals, on the other hand, function as regular pendulums and do not have to lift their bodies at each step. For moving upside-down hanging animals have to merely swing their bodies. In hanging animals, leg length and leg diameter can thus freely evolve by natural selection. Spiders are specially suited to test these hypotheses because living upside-down (i.e., hanging from their webs) has evolved independently a few times. Using independent contrasts we found that spiders that live upside-down have legs with higher length/diameter ratios than standing spiders. In addition, we report steeper positive allometries for leg length and diameter relative to body size in hanging spiders and found support for the hypothesis that natural selection has shaped these traits by showing that longer and thicker legs enhance swinging speed. We also show that due to their morphology, larger hanging spiders can no longer run efficiently standing on their legs. These findings have strong ecological implications.

08-32 Poster

HOW DO DIFFERENT METABOLIC RATES DURING THE WINTER AFFECT FITNESS?

Johan F. Nilsson [1], Jan-Åke Nilsson [1]

[1] Lund University, Animal Ecology, Ecology building, 223 62, Lund, Sweden

johan.nilsson@zooekol.lu.se

During its life time, an animal will experience periods with varying energy demands. This is of course also reflected in their metabolism, where it have been found that birds during i.e. breeding or migration increase their metabolic rate plentiful compared to most other periods of their lives. Overall it seams like birds have an astonishing ability to adjust their metabolic rate to meet up with the demands facing them. Little is however known about what consequences a varying metabolic level has for the animals in a longer time perspective. In this study, we measured the basal metabolic rate (BMR) during the winter time on a large number of wild blue tits (Parus caeruleus), in southern Sweden. These birds were then followed during their subsequent breeding attempts to see if the winter BMR in any way affected fitness related measures such as local survival, date of first egg, number of eggs, number of fledglings etc. This was done during two following seasons (2005 and 2006). To our knowledge this is the first study showing a link between the metabolic rate at one time of the year and the bird's fitness in the future, a question very important to answer to be able to understand life history trade-offs in birds.

08-33 Poster

WHY DO ANTS TEND APHIDS? INTERACTION VARIABILITY ACROSS AND WITHIN SPECIES.

Tom H. Oliver [1], James M. Cook [2], Simon R. Leather [1]

[1] *Imperial College London, Ecology and Evolution, Dept Biology, Silwood Park, Buckhurst Rd. Ascot, SL5 7PY, Ascot, UK*
[2] *University of Reading, School of Biological Sciences, Dept Biology, Silwood Park, Buckhurst Rd. Ascot, SL5 7PY, Reading, UK*

tom.oliver@ic.ac.uk

Aphid tending by ants (trophobiosis) shows a high degree of variability over a range of hierarchies- across and within species for both partners. Ecological context dependence studies can satisfactorily explain much population level variation. We describe how the phenotypic plasticity of certain aphid traits such as honeydew production help prolong an interaction with ants when it is beneficial. Differences in trophobiosis across species, however, require different evolutionary focused explanations. We use a genera level comparative analysis to determine ecological traits of ants that are associated with aphid tending. Several traits emerge, such as high levels of invasiveness, large colonies, arboreal nesting, polygyny and dominance, all of which are associated with trophobiosis. Comparative analyses do not differentiate between cause and effect, however, but simply detect association. We speculate as to what degree the ecological traits identified are preadaptations that allow monopolisation of honeydew producing resources, or whether some could actually be the selective consequences of ant: aphid interaction.

08-34 Poster

AGGRESSION AND EVOLUTIONARY STABILITY BETWEEN DIFFERENT MUTUALISTS OF ACACIA

Leonardo Ona-Bubach [1]

[1] *Max Planck Institute for Evolutionary Anthropology, Theoretical Biology, Deutscher Platz 6, 04103, Leipzig, Germany*

leonardo_bubach@eva.mpg.de

One of the most studied examples of mutualism is the one present between plants of the genus *Acacia* and several species of ants. Acacia take advantage of the services of the ants which patrol the plant and protect against the attack of herbivorous insects. The conflict appears because pollinators of *Acacia* may be attacked by the patrolling ants. How can this conflict be avoided?. In the present study we construct mathematical models to examine the conditions under which the three species can survive jointly without extinction events. Moreover, we test the sensitivity of the system to small changes in the physiological and behavioral parameters in the three species. We find that low levels of aggressive behavior are compatible with coexistence of the three species. We also propose different evolutionary scenarios to gain a better understanding of how ant aggression may evolve.

08-35 Poster

CAN INTERSPECIES EST DATA BE USED TO IDENTIFY GENES UNDER SELECTION WITHIN SPECIES?

Anna E. Palmé [1], Mark Wright [2], Outi Savolainen [3]

[1] *Uppsala University, Department of Evolution, Genomics and Systematics, Norbyvägen 18 D, 752 36, Uppsala, Sweden*
[2] *Cornell University, Department of Molecular Biology and Genetics, USA*
[3] *University of Oulu, Department of Biology, Finland*

anna.palme@ebc.uu.se

Identifying genes under positive selection has been a long standing goal in evolutionary biology, as these genes are the basis of adaptation. Even though many approaches have been used to identify genes under selection, this is still not an easy task. The main aim of this study is to investigate if it is possible to use interspecies EST data to predict selective patterns within species. We chose to use the Ka/Ks ratio (non-synonymous / synonymous divergence), as an indicator of selection as it is widely used and easily calculated. We analysed an EST dataset of 203 orthologous groups containing *Pinus pinaster, Pinus taeda, Picea glauca* and *Pseudotsuga menziesii*. Among these sequences one set of genes with high (0.20–0.52) and one with low (0.01–0.04) average Ka/Ks was chosen for sequencing in *Pinus sylvestris* populations. We see a strong correlation between Ka/Ks among different species and $\pi a/\pi s$ (non-synonymous / synonymous diversity) within *P. sylvestris*. This indicates conservatism in mode of selection and could simply be caused by the maintenance of the level of selective constraint. However, to investigate if the high Ka/Ks genes were more likely to be under positive selection than the low Ka/Ks genes we conducted several tests. The high group shows significantly more negative values of Tajima's D and related statistics and there was a positive correlation between these statistics and Ka/Ks. The HKA test indicates significant deviations from neutrality in the high Ka/Ks group but not in the low group. Taken together these results suggest that Ka/Ks from interspecies EST data can be used to identify a group of genes with a certain within-species diversity pattern and potentially an increased probability of being under positive selection. This could facilitate searches for genes that are adaptively important in many species.

08-36 Poster

THE DYNAMICS OF PHENOTYPE VARIATION OVER ONTOGENY AND ACROSS ENVIRONMENTS IN RESOURCE POLYMORPHIC ARCTIC CHARR (SALVELINUS ALPINUS)

Kevin J. Parsons [1], Skúli Skúlason [2], Moira M. Ferguson [1]

[1] *University of Guelph, Integrative Biology, Axelrod Bldg., N1G 2W1, Guelph, Canada*
[2] *Holar University College, 551, Sauðárkrókur, Iceland*

parsons@uoguelph.ca

A requisite of adaptive phenotypic evolution is that natural selection operates on variation throughout the ontogeny of an organism. Expression of variation is dependant on ontogenetic stage and environment and should be reduced by selection to canalize specialized phenotypes. Conversely, novel environmental conditions may increase variation through phenotypic plasticity. We test these predictions using two lake populations of polymorphic Arctic charr from Iceland that differ in their degree of ecological specialization. Individuals from the same ecomorph were reared with either benthic or limnetic prey. Offspring were sampled for morphometric analysis at two periods in the treatment (90 and 160 days). Differences in size and shape variation were detected over ontogeny, and across diet treatments. Such efforts could identify which ecomorphs possess evolutionary potential, and which ontogentic stages and environments allow selection to operate more readily on phenotypic variation.

08-37 Poster

INDIVIDUAL IDENTIFICATION OF CANTABRIAN BROWN BEAR (URSUS ARCTOS) THROUGH NON-INVASIVE GENOTYPING.

Trinidad Pérez [1], Fernando Vázquez [1], Ana Corao [1], Jesús Albornoz [1], Ana Domínguez [1]

[1] *Universidad de Oviedo, Biología funcional-Genética, Julian Clavería s/n, 33071, Oviedo, Spain*

mtpmendez@yahoo.es

Brown bear population from Cantabrian Mountains is subdivided in two subpopulations, both are threatened with extinction. This status led to the development of a brown bear recovery plan. To carry out this plan we need to increase our knowledge about the ecology, demography, and genetics of these subpopulations. Genetic data give us information about the genetic variability and structure of the population under study, and also let us to infer demographic and ecological data through individual identification. Non-invasive sampling allows individual identification of wild animals without having to catch, handle or even observe them. However genetic data generated using non-invasive samples present several drawbacks mainly related with the low quality/quantity of DNA recovered. This can lead to scoring errors and will produce incorrect genotypes. Different methods have been proposed to detect and to limit genotyping errors and their impacts on the subsequent analyses. This work presents the genetic data for both subpopulations of Cantabrian brown bear using non-invasive samples collected in the field during 2005-2006. It has been necessary to optimize a set of 18 mirosatellite loci and a sex marker to get a probability of identity among genotypes suitable to work with these small highly structured subpopulations. Loci microsatellites have been chosen from the ones available on the bibliography and then tested on individuals from both subpopulations (several multiplex reactions have been developed). Genotyping was made in two steps (a first conventional PCR followed by a second PCR using an internal marked primer) to increase the quality of the multilocus genotypes. Validation of the genotypes was made using a multi-tube approach. Different software programs were used to measure the error rate and the reliability of the different multilocus genotypes. Basic genetic data for both subpopulations were calculated using only those genotypes found reliable.

08-38 Poster

STUDYING SPECIATION OF PARASITOID COMMUNITIES: AN INTEGRATED EVOLUTIONARY AND ECOLOGICAL APPROACH

Saleta Perez Vila [1], Rampal Etienne [2], Han Olff [2], Leo W. Beukeboom [1]

[1] *University of Groningen, Centre for Ecological and Evolutionary studies, Evolutionary genetics, Kerklaan 30, 9751 NN Haren, GN, The Netherlands*
[2] *University of Groningen, Centre for Ecological and Evolutionary studies, Community and Conservation Ecology, Kerklaan 30, 9751 NN Haren, GN, The Netherlands*

s.perez.vila@rug.nl

Classically, biodiversity studies either have an evolutionary perspective (how do species originate and persist?) or an ecological perspective (how can so many species coexist?). Both perspectives should be combined, since biodiversity is considered the outcome of ecological interactions between species and population genetic and evolutionary processes. We aim to study the evolutionary and ecological processes and mechanisms that shape host-parasitoid communities. Insect parasitoids are involved in an arms race of adaptation and counter-adaptation with their hosts. This results in narrow niches for the parasitoids and rapid co-evolution. Because there are many independent lineages in which parasitism has evolved, hypotheses can be tested with replication. We first focus on the ecological and evolutionary interactions between sympatric *Nasonia* species that parasitize cyccloraphous fly pupae, and we search for answers to the following questions: What is the role of intracellular Wolbachia bacteria in causing diversity in parasitoids and hosts? How much niche differentiation exists between species and what are their host preferences? How much competition occurs between and within parasitoid species of the community? To what extent have adaptations evolved to prevent species hybridization? How much stochasticity affects speciation? Is there more speciation in the Neartic compared to the Paleartic zone, and if so, why? The next levels to incorporate will be other parasitoid species of the same hosts, such as larval parasitoids and competing pupal parasitoids, and parasitoid communities of other flies. Our methods will consist of empirical observations, natural and laboratory experiments and mathematical modelling.

08-39 Poster

EFFECTS OF EGG TESTOSTERONE LEVELS ON IMMUNITY, GROWTH AND SURVIVAL IN MAGPIE (PICA PICA) NESTLINGS

Marjo Pihlaja [1], Heli Siitari [1], Rauno V. Alatalo [1]

[1] *University of Jyväskylä, Departement of Biological and Environmental Science, P.O.Box 35, FIN-40014, Jyväskylä, Finland*

mapihla@bytl.jyu.fi

Maternally transmitted compounds in the eggs can be important in shaping offspring phenotype and in functioning as an efficient way to respond offspring to variable environmental conditions. In birds, there is relatively much variation between and within clutches in several maternally transmitted important compounds. Hormones, such as testosterone, can be very important for offspring development for its growth enhancing properties and in magpies (*Pica pica*) testosterone levels increase with laying order. Testosterone also might have negative effects e.g. suppressing immunity. We studied experimentally the effects of maternal testosterone deposition on nestling immunity, growth and survival in magpies by increasing egg yolk testosterone levels. Enhanced testosterone levels in later laid eggs decreased nestling growth compared to control nestlings from last laid eggs and early laid testosterone treated eggs, while control nestlings in later positions had higher growth rate compared to control nestlings from early laying positions. Moreover, enhanced testosterone levels suppressed survival of the nestlings originating eggs from late laying positions compared to all control nestlings and nestlings originating testosterone treated early laid eggs. Naturally strong sibling competition was relaxed in this experiment. Increased egg testosterone level decreased the level of antibodies in eggs available for nestlings. However, naturally last nestlings have higher levels of maternal antibodies and higher egg testosterone levels compared to first nestlings. Thus, mothers are compensating and even enhancing the level of antibodies available for last nestlings. It may be important since testosterone in high levels seems to have negative effects on growth and survival even without the stress of nestling competition. Our experiment verified the compensatory role of natural levels of testosterone in enhancing the growth of last hatchlings. Thus, in good conditions also the last nestlings are viable while in poor conditions brood reduction is fast.

08-40 Poster

MATERNAL INVESTMENT IN SONS REDUCES REPRODUCTIVE SUCCESS OF SUBSEQUENT OFFSPRING IN A PRE-INDUSTRIAL HUMAN POPULATION

Ian J. Rickard [1], Andrew F. Russell [1], Virpi Lummaa [1]

[1] *University of Sheffield, Department of Animal and Plant Sciences, Alfred Denny Building, Western Bank, S10 2TN, Sheffield, UK*

i.rickard@sheffield.ac.uk

Life-history theory predicts that reproductive events confer costs upon mothers. In line with this, many studies have shown reproduction to cause a decline in maternal condition, survival prospects or success in subsequent reproductive events. However, little attention has been given to the prospect of reproductive costs being passed onto subsequent offspring, despite the fact that parental fitness is a function of the reproductive success of progeny. Here we use pedigree data from a pre-industrial human population to compare offspring life-history traits and lifetime reproductive success according to the cost incurred by each individual's mother in the previous reproductive event. The cost differential we utilise is that of producing male over female offspring, which has been demonstrated in human and animal studies showing increased energy intake, reduced survival and lower future offspring birthweight in male-producing mothers. We show that those offspring born after elder brothers have lower lifetime reproductive success compared to those born after elder sisters, controlling for many confounding factors such as socio-economic status, ecological conditions and birth order. Our results demonstrate a maternal cost of reproduction manifested in reduced lifetime reproductive success of offspring. To our knowledge, this is the first time such a long-term intergenerational cost has been shown in a mammal species. We also investigate the potential mechanisms for this effect.

08-41 Poster

MITOCHONDRIAL PHYLOGEOGRAPHY OF CHAMOIS (RUPICAPRA SPP.) BASED ON CYTB.

Fernando Rodríguez [1], Sabine Hammer [2], Trini Pérez [1], Rita Lorenzini [3], Jacques Michallet [4], Franz Suchentrunk [5], Jesús Albornoz [1], Ana Domínguez [1]

[1] *Universidad de Oviedo, Biología Funcional - Genética, Julián Clavería s/n, 33071, Oviedo, Spain*
[2] *University of Veterinary Medicine, Clinical Immunology, Veterinaerplatz 1, 1210, Vienna, Austria*
[3] *Istituto Zooprofilattico Sperimentale dell'Abruzzo e del Molise 'G. Caporale', Savoyenstraße 1, 1210, Terama, Italy*
[4] *Office National de la Chasse et de la Faune sauvage, Veterinaerplatz 1, 1210, Eybens, France*
[5] *University of Veterinary Medicine, Research Institute of Wildlife Ecology, Savoyenstraße 1, 1160, Vienna, Austria*

rodriguezfernando@uniovi.es

Populations of chamois are distributed over most of the medium to high altitude mountain ranges of Europe. There are 10 distinct geographical populations of chamois that have been recognised as subspecies. Chamois populations have been grouped into two species, *Rupicapra pyrenaica* from south-western Europe and *R. rupicapra* from north-eastern Europe. We sequenced 349 nucleotides of the mitochondrial DNA *cytb* gene in a sample of 189 individuals that includes representatives of every subspecies, aiming to infer the phylogeographic structure of the genus and to revise *Rupicapra* systematic. The *cytb* sequences showed 20 haplotypes with 27 polymorphic sites. The data were used to construct a median joining network. The network shows the haplotypes grouped into three haplogroups that were named West, Central and East; according to the most frequent geographical origin of the individuals included in each haplogroup. The phylogenetic relationships among the three main clades can be interpreted on the basis of an East-West expansion and differentiation of mitochondrial lineages and the glacial barriers of the Alps and the Pyrenees. Postglacial recolonizations were mainly limited by the Alpine barrier. The phylogeny based on *cytb* sequences do not support the systematic of the genus. The two proposed species were polyphyletic; the clades West and Central are represented in both proposed species while the East clade is restricted to *R. rupicapra*.

08-42 Poster

RESOURCE COMPETITION TRIGGERS THE COEVOLUTION OF DEEP COROLLA TUBES AND LONG TONGUES

Miguel A. Rodriguez-Girones [1], Ana L. Llandres [1]

[1] *EEZA - CSIC, Functional and Evolutionary Ecology, General Segura 1, 04001, Almeria, Spain*

rgirones@eeza.csic.es

It is normally thought that deep corolla tubes evolve when the plant's successful reproduction is contingent on having a corolla tube longer than the tongue of the flower's pollinators. Combining optimal foraging theory and quantitative genetics in a spatially-explicit, individual-based model, we show that competition for resources can drive the coevolution between deep corolla tubes and long tongues in a community with two plant and two pollinator species. Variability in corolla depth favours tongue elongation in the pollinator species that can most easily afford it. Variability in tongue length leads, if pollinators are optimal foragers, to resource partitioning and assortative mating, which in turn promotes character displacement and differentiation of the corolla depth in the two plant species. This result is independent of any causal link between corolla depth and pollination success and highlights the importance of including ecological processes in evolutionary studies.

08-43 Poster

LABORATORY EVOLUTION OF TRADE-OFFS 2: COMBINING QUANTITATIVE GENETICS WITH FUNCTIONAL CONSTRAINTS TO PREDICT CHANGES IN DISPERSAL CAPABILITY

Derek A. Roff [1], Daphne J. Fairbairn [1]

[1] *University of California, Biology, Dept Biology, Universty of California, 92521, Riverside, USA*

derek.roff@ucr.edu

In a companion talk (Fairbairn and Roff) we described the adaptive loss of migratory capability in the wing dimorphic cricket, Gryllus firmus when maintained for ten generations in the laboratory with no opportunity for dispersal by flight. The general trajectory of this evolutionary response was predicted by our standard quantitative genetic model of the traits involved in the trade-off between fecundity and flight capability in female G. firmus. Here we extend this analysis to quantitatively predict the pattern of change in morphological and physiological traits using a quantitative genetic model combined with functional constraints. We use genetic estimates from a large-scale half-sib analysis to construct a quantitative genetic model incorporating fecundity, wing morph, flight muscle weight and functionality. In contrast to "traditional" quantitative genetic models our approach is designed to predict the changes in trait distributions, which we predict to vary from normal to highly bimodal. We show that this model correctly predicts the outcome of laboratory evolution and explains apparently anomalous behavior in the distribution of trait values. These results demonstrate the power of combining quantitative genetic and physiological approaches for understanding the evolution of complex traits as a result of changed ecological factors.

08-44 Poster

GENETIC VARIATION IN REPRODUCTIVE TRAITS OF A SMALL MAMMAL

Eero Schroderus [1], Minna Koivula [2], Esa Koskela [1], Tapio Mappes [1], Tuula A. Oksanen [1], Tanja Poikonen [1]

[1] *University of Jyväskylä, Biological and Environmental Science, P.O. Box 35, FIN-40014, Jyväskylä, Finland*
[2] *MTT Agrifood Research Finland, Animal Production Research, FIN-31600, Jokioinen, Finland*

eero.schroderus@bytl.jyu.fi

Understanding the sources of phenotypic variation is essential for the study of life-history evolution. Only variation by additive genetic effects can produce a selection response. Research has traditionally concentrated on direct additive genetic effects, but maternal genetic effects may explain more of the variation in many early life traits. Offspring number and size at birth are usually reported to have low heritabilities, and often a negative phenotypic correlation is observed between them. We estimated genetic parameters with the REML-animal model for litter size and individual birth size using data from a large laboratory colony of the bank vole (*Myodes glareolus*), a common rodent in the Palearctic region. Estimated direct heritabilities from the univariate models were low and maternal heritability for birth weight was higher than direct heritability. Bivariate models showed different heritability estimates. Most distinctly, the maternal heritability of birth weight increased. A strong negative genetic correlation was found between litter size and maternal effects for birth weight. Thus any evolutionary change in litter size tends to cause an opposite response in the offspring size via maternal effects. However, considerable amounts of genetic variation in maternal effects also exist for birth size independently of the litter size, thereby emphasizing the general importance of maternal effects in the evolution of birth size.

08-45 Poster

THE ADAPTIVE SIGNIFICANCE OF A MATERNAL EFFECT IN THE AFRICAN CICHLID SIMOCHROMIS PLEUROSPILUS

Francisca H. I. D. Segers [1], Barbara Taborsky [1, 2]

[1] *University of Bern, Dept. of Behavioural Ecology, Wohlenstrasse 50a, CH-3032, Hinterkappelen, Switzerland*
[2] *International Institute for Applied Systems Analysis (IIASA), Evolution and Ecology Program, Schlossplatz 1, A-2361, Laxenburg, Austria*

francisca.segers@esh.unibe.ch

In anticipation to an impoverished nurture environment of offspring, females of the Lake Tanganyika cichlid *Simochromis pleurospilus* increase the size of their eggs. In our study we aim to identify the ecological advantages that are associated with hatching from a relatively larger egg under bad food conditions. Juvenile *S. pleurospilus* were hand-raised from large and small eggs, respectively, until the age of three months. In a first step, we confirmed that egg weight is positively correlated with hatchling size due to a larger amount of yolk available for development. Afterwards we explored how long a maternal effect on egg size can benefit the offspring raised from large or small eggs when facing a rich or a poor nurturing environment. We performed repeated measurements on three parameters, which are likely to determine the survival of young in natural conditions. (i) We measured the body sizes and weights of juveniles of the four experimental groups to obtain growth trajectories. We examined the relative importance of egg size and nurture environment on (ii) swimming speed, a parameter which should increase survival chances in a predator encounter, and (iii) on the risk of being eaten by a predator, by assessing the willingness of the fish to forage under hazardous circumstances. Here we present the first results of this study and outline our future plans to unravel why egg size matters, when the going gets tough.

08-46 Poster

LOOKING AT HASHILAN MARSH "ECOLOGICAL, SOCIAL, AND ECONOMIC LANDSCAPES"

Keyvan Shamsi [1], Mehrnaz Mahdavi [1]

[1] *islamic azad university-kermanshah branch-iran, agronomy, poBox 67155-1774, Baghe nai street, 123321, kermanshah, iran*

shams2_k@yahoo.com

Hashilan Marsh is one of the most significant pools in Kermanshah province and west of country(iran).
This Marsh with approximate area of 450 hectar and low slope is located between khorain & Pirvays mountains and is watered by SabzAli Sarab. Climatic conditions of the marsh is generally under the overall conditions of the climate of westem part of state which is cold and semiarid.Given the situation of water source of the marsh, hydrological studies have shown that much of water of the pond is totally provided by SabzAli spring. Soils of the pond have been formed by reciprocal effects of soil-making factors including, mother materials, topography, climate, vegetative cover, and time.
Identified plants of the marsh included 44 families and 99 genuses and collectively were 122 species among of which 81 (66%) and 41 (44%) species were non-aquatic and aquatic, vespectedly. Plant diversity is higher at marginal, eastern, southern, and entrance areas of the pond. Some sorts of bacteria, phytoplanktons and zooplanktons, mollusks, annelids, fish, amphibian, fowls, and mammalia exist within the marsh.
A population about 5000 persons (12 villages) are living around the pond who are either directly or indirectly dependent on the marsh, although they have inflicted many irreparable damages to it in the last decades. Villagers living aroud the marsh cause it to be destroyed in such ways as expanding farmlands; removing its water for home and farming uses; grazing their cattles around the islands of the pond; hunting and fishing; collecting birds' eggs; outing and touring; releasing non-native species, contaminating the water in such different weys as washing animals, tractors, etc; dumping firing vegetation; and cutting and harvesting grasses and fodder. Twelve villages situated around or near the marsh have been investigated in terms of population; literacy level; employment rate; agriculture; stockbreeding; hunting; fishing; and touring. Ecological, social and economic aspect of pond are stated also in this paper.
Key words : Hashilan Marsh; Potencies; Ecology; Economy

08-47 Poster

CELL SIZE AS AN UNDERLYING FACTOR OF METABOLIC RATE SCALING: THE CASE STUDY IN EYELID GECKOS (SQUAMATA:EUBLEPHARIDAE)

Zuzana Starostová [1], Lukáš Kratochvíl [2], Lukáš Kubička [2], Marek Konarzewski [3]

[1] *Charles University, Department of Zoology, Viničná 7, 12844, Praha 2, Czech republic*
[2] *Charles University, Department of Ecology, Viničná 7, 12844, Praha 2, Czech republic*
[3] *University of Bialystok, Department of Animal Ecology, Świerkowa 20B, 15-950, Bialystok, Poland*

z.starostova@post.cz

It is well known that standard metabolic rate (SMR) scales with body mass. However, the precise value of a scaling coefficient and its theoretical elucidation is a matter of fierce discussion. Currently, two major alternative explanations exist: The first is based on fractal geometry and predicts ubiquity of scaling coefficient 3/4. The second one predicts that SMR scales with a coefficient between 2/3 and 1, depending on the cell surface to volume ratio, and potentially indirectly affected by genome size. Our aim was to study cell size/genome size variation as an underlying factor affecting interspecific variation in body size and SMR in the family Eublepharidae, the monophyletic group of geckos. Members of this clade exhibit large variation in body size. Previously we have found interspecific positive correlation of erythrocyte size and body size. In this project, we measured SMR at preferred temperatures in 14 forms of eyelid geckos. The interspecific allometric coefficient estimated by RMA regression was 0.64 ± 0.08 (S.E.). The mass-specific SMR correlates negatively to cell size, but there was no correlation between mass-specific SMR and genome size. In summary, our case study in eublepharids supports the role of cell size on SMR allometry.

08-48 Poster

GEOGRAPHIC VARIATION IN THE EVOLUTIONARY HISTORY OF HOST DEFENSE GENES

Peter Tiffin [1], David Moeller [1]

[1] *University of Minnesota, Plant Biology, 250 Biosciences, 55108, St. Paul, MN, USA*

ptiffin@umn.edu

Geographic variation in ecologically-important traits is common. For example, reciprocal transplant and common garden studies have detected ample evidence for geographic variation in patterns of selection and in host-defense phenotypes. These patterns have led to theories on the importance of geographic structure in shaping host and parasite evolution. To date, studies of coevolutionary interactions in a geographical context have focused on how current processes shape phenotypic evolution. To examine how geographic structure affects the long-term selective history of genes that underly host defense we analyzed sequence data from 15 defense and 7 non-defense from 6 geographically distinct sub-populations of the plant species Zea mays ssp. parviglumis. We detected strong evidence for a recent selective sweep at one defense gene in a single subpopulation and evidence that a second locus has experienced a global selective sweep. The time-scales captured by sequence data complicate differentiating whether this recent sweep is reflective of local adaptation, or ongoing species-wide adaptation.

08-49 Poster

ATMOSPHERIC CO2 EFFECTS ON SHORT-TERM PLANT EVOLUTION

Peter Tiffin [1], Jennifer Lau [1], Peter B. Reich [2], Ruth G. Shaw [1]

[1] *University of Minnesota, Plant Biology, 250 Biosciences, 55108, St. Paul, MN, USA*
[2] *University of Minnesota, Forest Resources, 115 Green Hall, 55108, St. Paul, MN, USA*

ptiffin@umn.edu

Extensive research has investigated the ecological impacts of increases in atmospheric carbon dioxide (CO_2) concentration. By contrast, we know little about the potential evolutionary impact of increased CO2. In a statistically powerful quantitative genetic experiment in which CO_2 concentrations were manipulated in a field setting we detected strong ecological but no evolutionary impacts of elevated CO_2 on *Arabidopsis thaliana*; plants produced ~25% greater biomass and fruits but patterns of selection, heritabilities, and genetic covariances between ecologically important traits were unchanged. However, a similar experiment conducted in the presence of competitors revealed that elevated CO_2 mitigated the effects of competitors as a selective force. In summary, our data from A. thaliana indicate that increasing concentration of atmospheric CO_2 may have little direct but strong indirect effects on the evolution of quantitative traits in plants.

08-50 Poster

THE ROLE OF REGULATORY GENES IN THE CICHLID FISH OF AFRICA

Katie Tindall [1], Domino Joyce [1], David Lunt [1]

[1] *University of Hull, Department of Biological Science, Cottingham Road, HU6 7RX, Hull, United Kingdom*

k.tindall@2004.hull.ac.uk

The cichlid fish of the African lakes are a classic example of adaptive radiation. Within the group there is a wide variety of morphology, behaviour and ecology, yet because the radiation has occurred in an evolutionarily short space of time, most members of the group are genetically similar, for example the haplochromine flock of Lake Malawi are have been found to have little or no phylogenetic signal in their nuclear genes. It has been suggested that regulatory evolution might be a driving force behind rapid changes in morphology. Evidence for this could include an increased rate of evolution across regulatory genes in cichlids that correlates with morphological diversity. To find such correlation, a computer application was produced which was able to design cross-species primers for any region of the cichlid genome, even where no cichlid data is currently available. Instead, the program uses data from orthologous genes in a number of other fish. Primers designed using this method were used to successfully amplify and sequence a number of previously unsequenced cichlid genes. The data arising from this molecular work, and published cichlid sequence data, was then analysed to examine patterns of rates of change in different gene classes both within cichlids and between cichlids and other fish.

08-51 Poster

PHYLOGENETIC RELATIONSHIPS OF THE PONTO – CASPIAN COROPHIIDS (AMPHIPODA, COROPHIIDAE)

Katya Uryupova [1], Nikolai Mugue [2]

[1] *Moscow State University, Biological, Leninskie Gory, GSP-1, 11991, Moscow, Russia*
[2] *Koltzov Institute of Developmental Biology RAS, Vavilova str., 26, 119334, Moscow, Russia*

ekurupova@mail.ru

The Caspian Sea and the Ponto-Caspian Region are the most interest places for evolutionists. It is inhabited by endemic crustacean fauna and amphipods are one of the most abundant groups here. They are numerous in other parts of the region, they are capable to active migration to new places and they have already dispersed to reservoirs and rivers at a short distance (for instance, Manych reservoir and upper Don River) from the Caspian Sea, as well as far beyond the limits of the Ponto – Caspian Region (the Baltic Sea, the Great Lakes in North America).Here we present results of our study of molecular phylogenetics, morphology and distribution of eight Ponto-Caspian species of genus *Chelicorophium* – *Ch. chelicorne* (Sars, 1895), *Ch. curvispinum* (Sars, 1895), *Ch. monodon* (Sars, 1895), *Ch. mucronatum* (Sars, 1895), *Ch. nobile* (Sars, 1895), *Ch. robustum* (Sars, 1895), *Ch. sowinskyi* (Martynov, 1924) and *Ch. spinulosum* (Sars, 1896). For comparative studies we used two species from other genus - *Corophium volutator* Pallas, 1766 (was sampled in the Sea of Azov) and *Crassicorophium bonelli* (Milne Edwards, 1830) (was sampled in the White Sea). Phylogeny based on both mitochondrial (COI) and nuclear (18sRNA) gene sequences reveal monophyletic origin of ponto-caspian species flock and it might have evolved autochthonously inside the region. *Ch. curvispinum* - *Ch. sowinskyi* and *Ch. chelicorne* - *Ch. spinulosum* form individual clades, and it confirms their high morphological similarity. 18S phylogenetic tree shows the same trend. We have established that corophiid flock is heterogeneous and each species differs from another. As a result we should suppose that each species have its own biological niche in this region. And the next question of us is *IS THAT REALLY THE CASE?* We just note that all species in different combinations are found with each other in the same biotopes. There is the mystery of speciation we should understand at a later time.

08-52 Poster

COMPETITION, COEXISTENCE AND GENEFLOW BETWEEN SYMPATRIC FLYCATCHERS.

Niclas Vallin [1]

[1] *Uppsala University, Dept. of Ecology and Evolution, Evolutionary Biology Centre/Dept. of Animal Ecology, Norbyv. 18D, 752 36, Uppsala, Sweden*

niclas.vallin@ebc.uu.se

Regional coexistence of similar competing species is more likely to occur if fluctuations in environmental conditions favour different species at different times or places. A life-history trade-off between interference competitive ability and robustness to harsh conditions is likely to promote a prolonged coexistence of two sympatric species of *Ficedula* flycatchers. The fitness of the more dominant collared flycatchers (*Ficedula albicollis*) is more sensitive to the seasonal decline in environmental conditions compared to pied flycatchers (*F. hypoleuca*), which may prevent competitive exclusion of the pied flycatcher. However, as the pied flycatcher becomes rarer the risk of hybridization increases, which may hasten local extinctions. I will consider effects of climate and habitat on the relative role of hybridization in driving patterns of extinction.

08-53 Poster

USING MOLECULAR DATA TO INTERPRET ECOLOGICAL GRADIENTS: AN INTERFACE BETWEEN GENETICS AND ECOLOGY

Katerina Vasileiadou [1], Elena Sarropoulou [1], Kostas Tsigenopoulos [1], Sophia Reizopoulou [2], Artemis Nicolaidou [3], Sotiris Orfanidis [4], Nomiki Simboura [2], Giorgos Kotoulas [1], Christos Arvanitidis [1]

[1] HCMR, IMBG, P.O.Box 2214, 71003, Heraklion, Greece
[2] HCMR, Institute of Oceanography, P.O.Box 712, 19013, Anavissos, Greece
[3] University of Athens, Zoology-Marine Biology, School of Biology, Panepistimiopoli, 15784, Athens, Greece
[4] NAGREF, Fisheries Research Institute, 64007, Kavala, Greece

k.vasileiad@gmail.com

Lagoons are shallow water bodies, semi- or completely isolated from the sea by sediment barriers, strongly influenced by adjacent sea, rivers and coast. Their small depth seems to be an important factor for temperature and salinity temporal and spatial variations, which are responsible for population fluctuation. Macrobenthos, shows low species diversity, a result of the response (/adaptation) of a few species to severe and highly variable conditions. Therefore, lagoons are a tempting field for the study of genetic adaptations and community behavior to extreme environmental conditions. Polychaetes, is the most diverse and abundant macrobenthic taxon, in the lagoons of Amvrakikos Gulf (NW Greece). Additionally, they are considered as well studied and they provide a good estimate of the benthic community showing similar trends to those produced by the total macrobenthic fauna. Until recently, faunal taxa were studied separately by ecologists and geneticists. However, using molecular data deriving from multispecies assemblages in order to test ecological theory has only recently been proposed in the scientific literature. As a first step, a comparison of the faunal patterns deriving from polychaete lagoonal taxo-communities to those deriving from molecular data from those species, is attempted in the course of this study. For this reason, mtDNA of the most abundant polychaetes from the Amvrakikos Gulf lagoons were used. Non-metric multidimensional scale (MDS) analysis was used to represent species and genetic diversity patterns, while 2nd stage MDS analysis was used for the comparison of the aforementioned patterns.

08-54 Poster

HABITAT DIFFERENCES DRIVING MULTIDIMENSIONAL NICHE DIFFERENTIATION

Thor Veen [1]

[1] University of Groningen, Theoretical Biology Group, Kerklaan 30, 9751 NN, Haren, The Netherlands

t.veen@rug.nl

Niche differentiation plays an important role in reducing interspecific competition between ecologically similar species, thereby promoting their coexistence. Niche differences have been most frequently described along single niche dimensions (e.g. spatial axis). However, it has been largely overlooked whether divergence of a single factor could underlie niche differentiation in multiple dimensions. Our data indicate that habitat differences found between two closely related species of *Ficedula* flycatchers (passerine birds) could result in niche differentiation in two dimensions. Firstly, habitat differences are likely to reduce the overlap of shared space which reduces interspecific interactions (*spatial* segregation). Secondly, we find a difference in seasonal abundance of an important food resource (caterpillars) between the habitat types, which is predicted to result in different timing of reproduction between the two species (*temporal* segregation). This is in accordance with the differences in mean breeding dates of the two species and the differences in reproductive success through the breeding season. Our findings suggest that selection acting on a single factor could facilitate species coexistence more than previously thought, due to the effect on multiple niche dimensions.

08-55 Poster

POPULATION DYNAMICS AND CONSISTENT INDIVIDUAL DIFFERENCES IN VITAL PARAMETERS

Yngvild Vindenes [1]

[1] *NTNU, Department of Biology, 7491 Trondheim, Norway*

vindenes@bio.ntnu.no

Consistent individual differences in vital parameters can affect population properties such as demographic variance, generation time, and effective population size. The dynamics of a population with consistent differences are described using a stochastic matrix model. Methods from the stochastic age-structured model are used to derive expressions for the demographic variance and generation time. A comparison model assuming a homogeneous population is also defined, with corresponding vital parameters. The results show that in general, the demographic variance depends on all vital parameter values, as well as on how these values are assigned to offspring. However, in the special case where the expected individual fitness is the same for all individuals, it is not affected by consistent individual differences. The generation time may increase compared to the homogeneous population, if individuals have different survival probabilities. An estimate of the variance effective population size of a fluctuating population with consistent individual differences (and two sexes) can be made based on diffusion theory. It depends on both the demographic variance and the generation time.

08-56 Poster

THE ECOLOGY AND EVOLUTION OF XYLARIA SPECIES ASSOCIATED WITH THE TERMITE-TERMITOMYCES MUTUALISM

Anna A. Visser [1], Alfons J. M. Debets [1], Thomas W. Kuyper [2], Rolf F. Hoekstra [1], Duur K. Aanen [1]

[1] *Wageningen University, Laboratory of Genetics, Arboretumlaan 4, 6703 BD, Wageningen, The Netherlands*
[2] *Wageningen University, Department of Soil Quality, Droevendaalsesteeg 4, 6708 PB, Wageningen, The Netherlands*

Anna.Visser@WUR.nl

Fungus-growing termites (subfamily Macrotermitinae) cultivate Basidiomycete fungi (of the genus *Termitomyces*) for food. They are mutually dependent. The cultivar is grown in single-strain monocultures that are clonally propagated within the termite nest. Since *Termitomyces* is a weak competitor and grown in monoculture, the question arises: what organisms threaten this mutualism and how are these organisms normally suppressed?

Species of the Ascomycete genus *Xylaria* seem to be associated with the mutualism. They are unnoticed in living termite nests. However, they occur in dead termite nests and on fresh nest material that is incubated in the absence of termites very frequently. What role do these *Xylaria* species play? Are they opportunists originating from the environment, or have certain species specialised in inhabiting termite nests?

To address these questions, termite mounds of three species of *Macrotermes* from different localities in South-Africa were investigated. *Xylaria* strains were isolated from the fungus garden and their distribution on different spatial scales was examined. Furthermore, phylogenetic relationships between the isolated *Xylaria* strains were reconstructed based on ITS sequences. The reconstructed *Xylaria* tree was compared with phylogenetic trees of the termites and *Termitomyces* to test for co-speciation.

08-57 Poster

SHRIMP-SPONGE ASSOCIATION FROM AN ANCIENT LAKE – THE FIRST KNOWN CASE IN FRESHWATER

Kristina Von Rintelen [1], Thomas Von Rintelen [2], Martin Meixner [3], Carsten Lüter [4], Yixiong Cai [5], Matthias Glaubrecht [6]

[1] Humboldt University Berlin, Museum of Natural History, Invalidenstrasse 43, 10115, Berlin, Germany
[2] Humboldt University Berlin, Museum of Natural History, Invalidenstrasse 4, 10115, Berlin, Germany
[3] SMB, Services in Molecular Biology, Invalidenstrasse 43, 10115, Rüdersdorf, Germany
[4] Humboldt University Berlin, Museum of Natural History, Breitscheidstrasse 70, 15562, Berlin, Germany
[5] National Parks Board, Biodiversity Centre, Invalidenstrasse 43, 10115, Singapore, Republic of Singapore
[6] Humboldt University Berlin, Museum of Natural History, 1 Cluny Road, 259569, Berlin, Germany

kristina.rintelen@museum.hu-berlin.de

Shrimp-sponge associations occur frequently in marine ecosystems, serving as model systems for the evolution of eusociality. The first known instance of such association in freshwater is described from an ancient lake in Indonesia. The recently described shrimp *Caridina spongicola* forms an exclusive and probably commensal association with a yet undescribed spongillinid sponge. Both show an extreme degree of endemism, being restricted to the outlet bay of Lake Towuti, the largest and the southermost of the Malili lakes in the central highlands of Sulawesi. Phylogenetic and ecological data suggest a comparatively recent origin of both taxa. Climatic fluctuations may have facilitated speciation and occasional hybridization of the shrimp species, which is derived from a rock-dwelling ancestor. Their extremeley localized occurrence in an increasingly disturbed area makes both taxa a conservation priority.

08-58 Poster

ADAPTIVE RADIATION IN ANCIENT LAKES – MULTIPLE COLONIZATION, TROPHIC SPECIALIZATION AND HYBRIDIZATION IN SPECIES FLOCKS OF THE FRESHWATER SHRIMP CARIDINA FROM SULAWESI

Kristina Von Rintelen [1], Matthias Glaubrecht [1], Christoph D. Schubart [2], Thomas Von Rintelen [1]

[1] Humboldt University Berlin, Museum of Natural History, Invalidenstrasse 43, 10115, Berlin, Germany
[2] University of Regensburg, Biology 1, Institute of Zoology, 93040, Regensburg, Germany

kristina.rintelen@museum.hu-berlin.de

Lacustrine radiations are great natural laboratories for the study of evolutionary processes. The Malili lake system and Lake Poso on the Indonesian island Sulawesi provide good model systems with several aquatic species flocks. Both host independent radiations of the freshwater shrimp *Caridina* (Decapoda, Atyidae). In stark contrast to the riverine species, these lacustrine representatives show flamboyant colour patterns. A combination of a molecular phylogeny (based on the mitochondrial genes 16S rRNA and cytochrome-oxidase-I) and a morphological revision of all species from the lakes and their respective drainage systems revealed several novelties: The Malili lake system has been colonized at least twice and one of its species flocks represents an intralacustrine adaptive radiation. These species have conspicuous and species specific colour patterns and show substrate-correlated morphological differences in their feeding appendages. In contrast the second Malili colonization consists of only one species, *Caridina lanceolata*, a generalist on various kinds of substrates and lacking a distinct colour pattern. While the Malili lakes host a truly adaptive radiation, the pattern gained for Lake Poso is rather more ambiguous. Although we also find species specific colour patterns and certain adaptive features, the phylogeny does not suggest an intralacustrine radiation, but the almost simultaneous appearance of several highly distinct and well supported genetic lineages, that may have evolved independently from riverine ancestors. We thus suggest quite similar environmental conditions can produce very different evolutionary patterns even in closely related organisms.

08-59 Poster

GENETIC STRUCTURE AND REPRODUCTIVE SUCCESS OF A HOMOPLOID HYBRID PINE PINUS DENSATA ON TIBETAN PLATEAU

Xiao-Ru Wang [1, 2], Xiao-Fei Ma [1], Jian-Feng Mao [1]

[1] *Institute of Botany, Chinese Academy of Sciences, State Key Laboratory of Systematic and Evolutionary Botany, 100093, Beijing, China*
[2] *Umeå University, Dept. Ecology and Environmental Science, 90187, Umeå, Sweden*

xiao-ru.wang@emg.umu.se

Pinus densata, a pine native to Tibetan Plateau, represents a good example of a homoploid hybrid speciation facilitated by adaptation to extreme environment and ecological isolation from the parents. Cytoplasmic markers are used to investigate the hybrid nature of *P. densata* populations. Analysis revealed that individual populations of *P. densata* have diverse genetic compositions, with varying degrees of genomic contribution from each parental species. These results suggest that populations of *P. densata* have unique evolutionary histories and most likely independent origins. Haplotype composition, gene genealogies and the levels and patterns of nucleotide variation at nuclear gene loci gave further support to the hybrid nature of *P. densata*. Allelic history suggests the ancient nature of the hybrid preceding elevation of the Tibetan Plateau. We detected more deviations from neutrality in *P. densata* than in the parental species. Thus, at least some of the evolutionary forces that have shaped the genetic variation in *P. densata* are likely to be different from those acting upon parental species. Comparative analysis on reproductive traits in *P. densata* and its parents showed little difference among the three pines, indicating a similar overall pollination and fertilization environment. Thus, despite the distribution on high plateau, natural populations of *P. densata* appeared to have normal levels of reproductive success, comparable to those of the two parental species each in their natural habitats. These findings shed lights on the processes that lead to the successful hybrid speciation in a novel habitat that is ecologically and spatially inaccessible to any of the parental species.

08-60 Poster

COORDINATION AND BEHAVIOURAL TRANSITIONS AMONG BROOD-REARING EIDER FEMALES

Markus Öst [1], Tekla Tierala [1]

[1] *University of Helsinki, Biological and Environmental Sciences, PO Box 65, Viikinkaari 1, 00014, Helsinki, Finland*

markus.ost@helsinki.fi

New research into activity coordination within social groups has revealed that earlier empirical data often fail to satisfy the assumptions of theoretical models. For example, foraging and antipredatory vigilance are often not mutually exclusive. Theories addressing which group member should decide upon behavioural transitions have lately emerged; however, theoretical predictions have not been evaluated in study systems providing large natural variation in individual energetic states and social dominance, two factors presumed to be important. Brood-rearing coalitions of female eiders (*Somateria mollissima*) are well suited for exploring group coordination. Females are unable to detect airborne duckling predators (gulls) while diving for food, so if all females dive synchronously, the ducklings are left exposed to predators. Since incubation is accomplished without feeding, the body conditions of brood-tending females are highly variable, and females show a dominance hierarchy. We explored the factors influencing the coordination of diving within brood-rearing coalitions, and the individual characteristics governing the initiation of foraging cycles. Perhaps unsurprisingly, the proportion of total diving time that all females were submerged decreased with female group size, indicative of enhanced duckling protection. This proportion also decreased with the ratio of ducklings to tending females, while it showed a nonsignificant tendency to increase with the number of group outsider females present. Female aggression and spatial centrality, two measures of female dominance, both independently increased the probability of initiating a foraging cycle, while body condition, size, age and female group size were unrelated with foraging cycle initiation. Our results demonstrate that females are capable of adjusting the timing of their activities with respect to other group members both in response to variation in duckling vulnerability and the social dominance relationships.

9

Evolution of diversity in heterogenous environments

Tuesday August 21 *Location:* Ekonomikum 4

Symposium 9: Evolution of diversity in heterogenous environments

ORGANIZERS: Sara Magalhães, Instituto Gulbenkian de Ciencia, Portugal
Virginie Ravigné, CIRAD, Montpellier, France
Ophélie Ronce, Université de Montpellier II, France

09.45-10.15	**Graham Bell** (invited) Adaptation to complex environments
10.15-10.45	**Thomas Lenormand** (invited) The reinforcement of local adaptation
10.45-11.05	**Claus Rueffler** The interplay between behaviour and morphology in the evolutionary dynamics of resource specialization
11.05-11.35	*Coffee*
11.35-11.55	**Adrien Frantz** The importance of phenotypic traits other than performance and preference in the process of ecological specialization
11.55-12.15	**Frederic Austerlitz** Evolution of genetic diversity and differentiation for genes involved in regulation networks
12.15-12.35	**Thomas Bataillon** The ecological genetics of new mutations
12.35-14.00	*Lunch*
14.00-14.20	**Greg McInerny** Mutation fixation across range limits: consequences for range dynamics and responses to climate change
14.20-14.40	**Bénédicte Rhone** Flowering time trait, gene and microsatellite differentiation among experimental populations of wheat evolving in contrasted environments
14.40-15.00	**Patrick Venail** Functional diversity and productivity peak at intermediate levels of dispersal in evolving metacommunities
15.00-15.20	**Alex Hall** How does resource supply affect evolutionary diversification?
15.20-16.00	*Coffee*

09-01 Talk

ADAPTATION TO COMPLEX ENVIRONMENTS

Graham Bell [1]

[1] *McGill University, Biology, 1205 ave Docteur Penfield, H3A1B1, Montreal, Canada*

graham.bell@mcgill.ca

Most microcosm experiments with microbes are done in simple media with a single limiting carbon source. Most natural populations live in complex media with no single limiting substrate. Selection in complex environments might lead to a single universal generalist or to a range of narrowly specialized types. The outcome of experiments suggests an intermediate situation, the evolution of overlapping imperfect generalists.

09-02 Talk

THE REINFORCEMENT OF LOCAL ADAPTATION

Thomas Lenormand [1]

[1] *CEFE-CNRS, Montpellier, France*

Thomas.LENORMAND@cefe.cnrs.fr

In general, individuals who have survived to reproduce have genotypes that work relatively well under local conditions. Migrating or sending offspring elsewhere is likely to decrease an individual's fitness or that of its offspring. Besides reducing dispersal, there are other ways to reinforce local adaptation: it is possible to recombine less, to self or to mate assortatively. Even if it is true that local adaptation selects against each of these isolation mechanisms, they do not evolve in the same way. I will try to compare them and discuss the plausibility of these different routes to reinforcement of local adaptation.

09-03 Talk

THE INTERPLAY BETWEEN BEHAVIOR AND MORPHOLOGY IN THE EVOLUTIONARY DYNAMICS OF RESOURCE SPECIALIZATION

Claus Rueffler [1], Hans A. J. Metz [2, 3], Tom J. M. Van Dooren [2]

[1] *University of Toronto, Department of Ecology and Evolutionary Biology, 25 Harbord Street, M5S 3G5, Toronto, Canada*
[2] *Leiden University, Institute of Biology Leiden, Kaiserstraat 63, 2311 GP, Leiden, Netherlands*
[3] *International Institue of Applied Systems Analysis, Evolution and Ecology Program, 2361, Laxenburg, Austria*

rueffler@zoo.utoronto.ca

We analyze the consequences of diet choice behavior for the evolutionary dynamics of foraging traits by means of a mathematical model. The model is characterized by the following features: Consumers feed on two different substitutable resources that are distributed in a fine grained manner. Consumers decide upon encounter with a resource item whether to attack it or not so as to maximize their energy intake. Simultaneously, evolution occurs in traits affecting resource specific handling times and search efficiencies. For each trait, a trade-off exists between the consumer's ability to forage on the alternative resources. The model predicts that flexible diet choice behavior can guide the direction of evolutionary change and that flexible behavior can mediate coexistence of different consumer types. Such polymorphisms can evolve from a monomorphic population at evolutionary branching points and also at points where a small genetic change in a trait can provoke a sharp instantaneous and non-genetic change in choice behavior. In the case of weak trade-offs, the evolutionary dynamics of a dimorphic consumer population can lead to alternative evolutionarily stable communities. The robustness of these predictions is checked with individual-based simulations and by relaxing the assumption of optimally foraging consumers.

09-04 Talk

THE IMPORTANCE OF PHENOTYPIC TRAITS OTHER THAN PERFORMANCE AND PREFERENCE IN THE PROCESS OF ECOLOGICAL SPECIALIZATION

Adrien Frantz [1], Manuel Plantegenest [2], Jean-Christophe Simon [2]

[1] *Université Montpellier 2, Institut des Sciences de l'Evolution de Montpellier, UMR CNRS 5554, 34095 Montpellier Cedex 05, France*
[2] *UMR INRA/Agrocampus Rennes, Biologie des Organismes et des Populations appliquée à la Protection des Plantes, 35653, Le Rheu Cedex, France*

frantz@isem.univ-montp2.fr

The evolution of reproductive isolation between sympatric populations has long constituted one of the most puzzling issues in evolutionary biology. Recently, sympatric speciation has gained strong support owing to studies on ecological specialization of populations to alternative habitats. This process involves the selection of coadapted traits affecting habitat use, among which performance and preference have been given full attention.

Habitat use however includes various other phenotypic traits. How such traits can be affected by the specialisation and how these traits can potentially influence the divergence itself remain poorly known. We investigated this issue in the pea aphid, which exhibits a tremendous phenotypic variability and lives in contrasted habitats.

Our study shows that sympatric pea aphid populations constitute three genetic clusters respectively living on (i) pea and faba bean, (ii) on red clover, and (iii) on alfalfa. These clusters are strongly differentiated on each of the phenotypic traits measured, probably due to contrasted levels of habitat heterogeneity (annual vs. perennial). In addition, these traits are likely to strongly influence gene flow between host populations. Aphids from pea and faba bean produce sexual morphs and winged males in high proportions, which may promote population mixing and limit host specialisation. Those from clover and alfalfa show the opposite pattern that may favour host specialisation. Finally, each host population specifically harbours one given facultative endosymbiont that could limit exchanges and favour the maintenance of population differentiation. Overall, our study points out the importance of phenotypic traits other than performance and preference in the process of specialisation to alternative habitats.

09-05 Talk

EVOLUTION OF GENETIC DIVERSITY AND DIFFERENTIATION FOR GENES INVOLVED IN REGULATION NETWORKS.

Frederic Austerlitz [1], Julien Guglielmini [2]

[1] *CNRS - Universite Paris-Sud, Laboratoire Ecologie, Systematique et Evolution, Batiment 360, F-91405, Orsay, France*
[2] *Free University of Brussels (ULB), Unit of Evolutionary Genetics, Institute of Molecular Biology and Medicine (IBMM), CP300, Rue Jeener & Brachet 12, B-6041, Gosselies, Belgium*

frederic.austerlitz@u-psud.fr

There have been recently a number of experimental studies on the evolution of genes involved in regulation networks, which have shown that many of these genes are submitted to selective pressures. A theoretical framework is clearly needed to better understand these selective pressures. We develop here a model that considers a quantitative trait that is coded by a set of loci, which regulate each other through positive or negative interactions. We simulate either isolated populations or populations connected through migration, under disruptive selection. We show that an increasing intensity of selection yields an increased level of regulation between the loci. More importantly, we show that among the loci of the regulation network, the loci that answer the more to selection are the ones that have evolved the stronger regulatory action on the other genes and that this is specifically true for an intermediate intensity of selection. Our model thus clearly shows that regulatory genes are expected to be under strong selective pressures and that selection acts principally on the more upstream genes within the network. This has been observed for several regulatory genes in natural populations. Our results have important consequences in the context of the search of genes under selection through genome scans: the genes that are the more likely to be detected under this framework are the more regulatory ones.

09-06 Talk

THE ECOLOGICAL GENETICS OF NEW MUTATIONS

Rees Kassen [1], Thomas Bataillon [2]

[1] *University of Ottawa, Department of Biology, K1N 6N5, Ottawa, Canada*
[2] *University of AArhus, Genetics and Ecology, 8000C, AArhus, Denmark*

tbata@daimi.au.dk

The extent to which a population diverges from its ancestor through adaptive evolution
depends on variation supplied by novel beneficial mutations. In recent empirical work using the bacterium model Pseudomonas fluorescens we have shown, in line with theory, that the distribution of fitness effects among beneficial mutations is both exponential, with many small fitness effects and few large ones, and invariant, in the sense that this distribution is always exponential regardless of the starting fitness of the ancestral type. Here we extend this work to investigate in detail the pleiotropic consequences of single-step mutations across a wide range of environments. We show specifically that, when fitness is measured across 95 different carbon substrates, novel beneficial mutations contribute to both the main effect genetic variance and genotype-by-environment interaction for fitness but this variation is not associated with large costs of adaptation. This result suggests that the costs of adaptation, when they do arise, are likely to be due to the cumulative effects of many beneficial mutations rather than just a few.

09-07 Talk

MUTATION FIXATION ACROSS RANGE LIMITS: CONSEQUENCES FOR RANGE DYNAMICS AND RESPONSES TO CLIMATE CHANGE.

Greg J. McInerny [1], John R. G. Turner [2], Hor Y. Wong [2], Tim G. Benton [2], Justin M. J. Travis [3]

[1] *Centre for Ecology and Hydrology, CEH Banchory, Hill of Brathens, Banchory, AB31, Aberdeenshire, UK*
[2] *University of Leeds, Institute of Integrative and Comparative Biology, L C Miall Building, LS2 9JT, Leeds, UK*
[3] *University of Aberdeen, School of Biological Sciences, Zoology Building, AB24 2TZ, Aberdeen, UK*

gmci@ceh.ac.uk

In a patch occupancy model, we explore how ecological structure modulates the fixation of a mutation that has the potential to allow range expansion. Our results show fixation probabilities are intimately linked with the spatial structure generated by occupancy and dispersal along an extinction gradient. We demonstrate that the location of a mutations origin determines the probability of fixation and necessitates an explicit understanding of spatial patterning. A directional shift in the extinction gradient simulates conditions expected during climate change. We show how the orientation of climate change in relation to the range limit produces large and contrasting effects on the spatial structure of occupancy and fixation of the mutation. The results provide a substantial contribution to understanding (1) ecological constraints on evolutionary processes at range limits and (2) diversification of populations in static climates and during climate change.

09-08 Talk

FLOWERING TIME TRAIT, GENE AND MICROSATELLITE DIFFERENTIATION AMONG EXPERIMENTAL POPULATIONS OF WHEAT EVOLVING IN CONTRASTED ENVIRONMENTS

Bénédicte Rhone [1], Isabelle Goldringer [1], Nathalie Galic [1], Isabelle Bonnin [1]

[1] *INRA, UMR de Génétique Végétale, Ferme du Moulon, 91190, Gif-sur-Yvette, France*

rhone@moulon.inra.fr

Local adaptation arising from spatial and temporal heterogeneity in selection pressures acting on heritable traits is the main force shaping the phenotypic diversity in natural populations. The influence of local selection on populations can be inferred by comparing the genetic differentiation of potentially selected traits with the genetic differentiation of neutral molecular makers. However, few is known on the evolution of diversity and spatial structure for genes involved in the control of adaptive traits which may depend on the level of linkage disequilibrium between loci. In this study, we compare the three levels of differentiation (traits *vs.* markers and genes *vs.* makers) observed in experimental populations of the selfing wheat to characterize the level and heterogeneity of selection on genes involved in population adaptation. The studied populations evolved since 1984 in a multi-site experimental network in France under the influence of natural selection and drift. In response to local environmental conditions, populations were differentiated for traits such as flowering time after 10 generations only. In annual plant species, flowering time is a major adaptive trait that synchronizes the initiation of reproduction with the seasons ensuring reproductive success under favourable environmental conditions. The molecular control of flowering time is becoming more documented in model species (*A. thaliana*, rice). Based on this knowledge and on recent publications on wheat, we identified candidate genes associated with the variation in flowering time and analysed the evolution of their genetic variability during subsequent generations (2, 7 and 12) in three populations grown in contrasted environments (Vervins 49.5°N, 3.5°E, Le Moulon 48.4°N, 1.4°W, Toulouse 43.4°N, 1.3°E). These populations were also characterized for earliness and microsatellites markers. Differences between the three levels of differentiation at spatial and temporal scales will be discussed.

09-09 Talk

FUNCTIONAL DIVERSITY AND PRODUCTIVITY PEAK AT INTERMEDIATE LEVELS OF DISPERSAL IN EVOLVING METACOMMUNITIES

Patrick Venail [1]

[1] *Université Montpellier 2, Institut des Sciences de l'Evolution (UM2-CNRS), Place Eugène Bataillon, CC 065, 34 095 Montpellier cedex 5, France*

pvenail@univ-montp2.fr

The relationship between species richness and ecosystems properties such as productivity is central to our understanding of biodiversity (Loreau, 2001, Hooper 2005). A consensus has emerged that positive relationships can arise through complementarity or selection effects (Loreau, 2001). However the joint effect on ecosystem properties of ecological and evolutionary mechanisms that control diversity has yet to be considered. Here we show using experimental evolution of the bacterium *Pseudomonas fluorescens* SBW25 that limited dispersal in a heterogeneous metacommunity leads to the evolution of maximal functional diversity and productivity at the regional scale. As predicted by models of niche differentiation, higher complementarity in resource use strategies allows greater coverage of the heterogeneous environment leading to higher productivity (Tilman 1997, Loreau 1998). Our results demonstrate for the first time that a positive relationship between functional diversity and productivity can evolve *de novo* through adaptive radiation into complementary types. Dispersal and environmental heterogeneity determine the evolution and maintenance of functional diversity that in turn determine ecosystem productivity levels.

09-10 Talk

HOW DOES RESOURCE SUPPLY AFFECT EVOLUTIONARY DIVERSIFICATION?

Alex R. Hall [1], Nick Colegrave [2]

[1] *University of Edinburgh, Institute of Evolutionary Biology, Room 413, Ashworth Laboratories, EH9 3JT, Edinburgh, United Kingdom*
[2] *University of Edinburgh, Institute of Evolutionary Biology, EH9 3JT*

alex.hall@ed.ac.uk

The availability of different resources in the environment can play a central role in the evolution of diversity. A range of evidence points to a peak in diversity at intermediate levels of resource supply, which has been explained previously in the context of selection acting in spatially heterogeneous environments. Here we propose an alternative mechanism to explain the relationship between resource supply and diversification, based on selection for exploitation of different resources. This mechanism was tested by a selection experiment using the bacterium Pseudomonas fluorescens in spatially uniform environments over a wide range of resource supply rates. Results show that the evolution of specialists and generalists varies with resource supply rate, and that niche diversification does indeed peak at intermediate levels. We suggest that this unimodal relationship is due to evolutionary diversification that is driven by competition for resources but constrained by the ecological opportunity represented by different resource types. These processes may underlie some general patterns of diversity, including latitudinal gradients in species richness and the effects of anthropogenic enrichment of the environment.

09-01 Poster

EXPLORING REPRODUCTIVE POLYMORPHISM, PLOIDY DIFFERENCES AND GENETIC VARIABILITY IN EUROPEAN E. VIRENS OSTRACODS

Sofia Adolfsson [1], Yannis Michalakis [1], Jukka Jokela [2]

[1] *IRD/CNRS, Genetique et Evolution des Maladies Infectieuses, Avenue Agropolis 911, 34394, Montpellier, France*
[2] *ETHZ/EAWAG, Aquatic ecology, Uberlandstrasse 133, 8600, Dubendorf, Switzerland*

sofia.adolfsson@eawag.ch

An elevation in ploidy level often accompanies the transition from sexual to asexual mode of reproduction, yet the role of ploidy in the evolutionary maintenance of populations is still not clear. Its impact is sought in the freshwater ostracod *Eucypris virens* which has a wide geographical distribution and exhibit variability in ploidy and mode of reproduction. The increased heterozygosity of triploids has the potential to increase adaptability to changing and novel environments compared with diploid progenitors. This in combination with uniparental reproduction will positively and markedly effect migration abilities.

However, in this species there is no evidence for particular triploid clones being more geographically widespread than diploid clones. In fact clones with both ploidy levels seem to be localized, undermining the idea that there would be one or several generalist clones. Moreover, only triploid populations are found north of the Alps while around the Mediterranean we see triploid asexual populations, diploid asexual populations, diploid sexual populations and mixtures of the three, which supports greater migration abilities due to triploidy rather than asexuality. Triploid populations that live very close to sexual populations harbour more genotypic variability in comparison to geographically distant triploids, which suggests either frequent spin-offs of clones from sexuals or competition driven maintenance of high triploid asexual genotypic diversity in southern Europe.

09-02 Poster

THE EFFECTS OF MATERNAL HOST PLANT SPECIES AND SELFING ON HEMIPARASITIC RHINANTHUS SEROTINUS

Riitta K. Ahonen [1], Inka Kynsilehto [1], Pia K. Mutikainen [2, 1]

[1] *University of Oulu, Department of Biology, P.O. Box 3000, FI-90014, Oulu, Finland*
[2] *ETH Zürich, Institute of Integrative Biology, P.O. Box 3000, FI-90014, Zürich, Switzerland*

riitta.ahonen@oulu.fi

Self-pollination is a common phenomenon in many plant species. However, it often has deleterious genetic effects, namely inbreeding depression. However, these effects may in some cases be countered if harmful alleles are purged in inbred lines. Performance of generalist hemiparasitic plant varies according to the host plant species that they are attached to. We studied the effects of self-pollination and host plant species of a hemiparasitic maternal plant, *Rhinanthus serotinus*, on the performance of the offspring grown on two host species *Trifolium pratense* and *Agrostis capillaris*. We grew *R. serotinus* in greenhouse on these two hosts and pollinated (self or cross) them by hand. In addition, we pollinated individuals in two field populations and collected seeds of naturally open pollinated individuals. We measured the reproductive output of maternal *R. serotinus*, and further, the differences in germination, infection, and fitness traits of the offspring in these different treatments. The results suggest that host species affected the number of flowers and seed production of the maternal plants, but selfing had no effect on the number or biomass of produced seeds.

09-03 Poster

THE FLY THAT CAME FROM THE WEST: DROSOPHILA SUBOBSCURA IN ARGENTINA

Pedro F. Iriarte [1], Joan Balanya [2], Marta Pascual [2], Francesc Mestres [2], Esteban Hasson [3], Antonio Fontdevila [4], Luis Serra [2]

[1] *Universidad Nacional de Mar del Plata, Departamento de Biología, Funes 3250, 7600, Mar del Plata, Argentina*
[2] *Universitat de Barcelona, Grup de Biologia Evolutiva, Departament de Genètica, Av. Diagonal, 645, 08028, Barcelona, Spain*
[3] *Universidad de Buenos Aires, Departamento de Ecología, Genética y Evolución, Ciudad Universitaria, 1428, DF Buenos Aires, Argentina*
[4] *Universitat Autònoma de Barcelona, Grup de Biologia Evolutiva, Departament de Genètica i Microbiologia, Edifici C, 08193, Bellaterra, Spain*

jbalanya@ub.edu

The Palaearctic species *Drosophila subobscura* has colonized the Pacific coast of Chile since the late 70's and of North America, from California to British Columbia, since the early 80's. It was first detected in the Atlantic coast of Argentina in 1984, but the question remained whether the species formed established populations in the area and, if so, whether these populations represented a new colonization event from the Old World. Two samples from Maipú and Mar del Plata, respectively, collected in November 2005 were analyzed for their chromosomal and microsatellite allele polymorphisms as well as for the presence of a lethal allele typical of the American colonizing populations. The results show that these populations are well established in the area and that all the genetic markers examined present the same characteristics as those of the American populations analyzed previously, rejecting the hypothesis of a new introduction of the species. Moreover, a mild secondary bottleneck is detected when comparing the microsatellite data with those of the Chilean populations, suggesting that the Argentinian populations are the result of the expansion of the species from the colonized areas in the west.

09-04 Poster

EFFECT OF SPATIAL PATTERNS ON THE EVOLUTION OF LIFE HISTORY TRAIT DIVERSITY

Lucie Büchi [1], Alexandre H. Hirzel [1]

[1] *University of Lausanne, Department of Ecology and Evolution, Biophore, Quartier Sorge, 1015, Lausanne, Switzerland*

Lucie.Buechi@unil.ch

Hubbell's neutral theory of biodiversity can successfully predict broad community patterns such as abundances curves or diversity. However it cannot compete with niche-based theories to explain more specific patterns, where species' traits play a major role (*e.g.* competition or dispersal). With the current threat on species diversity, it is of crucial importance to determine what are the limits of application of each theory and how they are affected by environmental issues.

This work focuses on community patterns at the level of the species. We investigate how environmental factors, such as disturbances, heterogeneity and spatial autocorrelation, influence in communities the distribution of some species' traits (*e.g.* ratio of dispersers vs. philopatrics, generalists vs. specialist). We address these questions with numerical simulations where species compete for a shared resource in a spatially structured landscape. Each site in the landscape is characterised by a limited amount of resources and by an environmental variable. The spatial distribution of this variable is homogeneous or heterogeneous, with varying autocorrelation. Species differing by their niche optimum and breadth, dispersal ability, competitivity and reproductive investment, are generated and released in a landscape where they compete for resources. At each time step, a proportion of all individuals dies, and disturbances kill all individuals in some randomly drawn sites. The system is let to evolve until it reaches equilibrium.

We focus here on the evolution of dispersal in various kinds of landscapes, offering interesting insights about the interaction between landscape heterogeneity, disturbances and species' life history traits. In particular our results suggest that the amount of disturbances and the environment spatial autocorrelation strongly affect the proportion of short and long dispersers in the equilibrium community. And this is likely to influence landscape connectivity, and in turn community diversity or species abundances.

09-05 Poster

THE EVOLUTION OF HABITAT PREFERENCE

Angeles De Cara [1], Nick H. Barton [1]

[1] *University of Edinburgh, Institute of Evolutionary Biology, Ashworth Laboratories, King's Buildings, EH9 3JT, Edinburgh, United Kingdom*

Angeles.deCara@ed.ac.uk

Habitat preference is relevant to the evolution of specialisation, sympatric speciation and the maintenance of genetic variation. Yet these areas are rarely brought together. In this work, we explore the conditions for habitat preference to evolve, and how it affects reproductive isolation. For that purpose, we have combined game theory with population genetics. Our model is of two niches, and we have derived fairly general conditions for the maintenance of a polymorphism of one and two types. These conditions determine whether a generalist can invade a single specialist, or whether only a polymorphism of two specialists can be maintained. We mostly explore the consequences of this model for sympatric speciation and maintenance of polymorphisms.

09-06 Poster

RE-EVOLUTION OF SEX BREAKS DOLLO'S LAW – THE ROLE OF HETEROGENEOUS ENVIRONMENTS

Katja Domes [1], Roy A. Norton [2], Mark Maraun [1], Stefan Scheu [1]

[1] *University of Technology, Zoology, Schnittspahnstrasse 3, 64287, Darmstadt, Germany*
[2] *State University of New York, College of Environmental Science and Forestry, 1 Forestry Drive 16, 13210, Syracuse, USA*

domes@bio.tu-darmstadt.de

The dominance of sexual reproduction is still an unresolved enigma in evolutionary biology. Strong advantages of sex have to exist since only a few parthenogenetic taxa persist over evolutionary timescales. Oribatid mites (Acari) include outstanding exceptions to the rule that parthenogenetically reproducing taxa are of recent origin and doomed to extinction. In addition to the existence of large parthenogenetic clusters in oribatid mites, phylogenetic analyses of this study and model-based reconstruction of ancestral states of reproduction imply that Crotoniidae have re-evolved sexuality from parthenogenetic ancestors within one of those clusters. This reversal in reproductive mode is unique in animal kingdom and violates Dollo's law that complex ancestral states can never be reacquired. The re-evolution of sexuality requires that ancestral genes for male production are maintained over evolutionary time. This likely is true for oribatid mites since spanandric males exist in various species, although mechanisms that enable the storage of genetically ancestral traits are unclear. Also enigmatic are the environmental circumstances under which a reversion to sex is favored. While parthenogenesis dominates in soil-dwelling oribatid mite communities, species inhabiting the bark of trees or mosses are almost exclusively sexual. This phenomenon suggests that sexual reproduction is necessary for coping with more heterogeneous environments or increased exposure to antagonists in aboveground habitats.

09-07 Poster

TWO ADAPTATIONS TO ENVIRONMENTAL UNCERTAINTY: GENERALIZATION VERSUS DIVERSIFICATION

Matina C. Donaldson [1, 2], Carl T. Bergstrom [1], Michael Lachmann [2]

[1] *University of Washington, Department of Biology, 24 Kincaid Hall; Box 355320, 98195, Seattle, WA, USA*
[2] *Max Planck Institute for Evolutionary Anthropology, Department of Evolutionary Genetics, Deutscher Platz 6, 04103, Leipzig, Germany*

matina@u.washington.edu

Organisms inhabiting a changeable, unpredictable environment face a special adaptive challenge. One response is to become a generalist, capable of surviving in wide range of conditions, yet never excelling in any. Another is to produce many diverse offspring specializing in different conditions. This latter kind of adaptation, known as bet-hedging, is quite costly because many offspring end up facing conditions they are not equipped to handle. Whether a population adapts to environmental uncertainty by generalizing or by diversifying depends first of all on how the risk is distributed across individuals and generations. Misfortune befalling single individuals, like predation, favors the evolution of a single type whose average fitness is high. In such cases, bet-hedging is never adaptive. Here we focus instead on large-scale disasters like drought, which have a much greater impact, and require more desperate measures—like bet-hedging. We define a quantitative measure of the degree to which an individual is specialized in the various environmental conditions it may experience, based on the proportion of reproductive effort invested in each environment. Using this measure, the optimal strategy is surprisingly easy to define: one should specialize in each environment according to how often it occurs. This optimal level of specialization may be achieved by producing many offspring highly specialized for different environments, or by a single more generalist type with intermediate fitness in all environments. This framework allows us to directly compare the strategies of generalization and diversification, and make predictions about the circumstances favoring each.

09-08 Poster

COEXISTENCE OF PHYTOPLANKTON SPECIALISTS AND GENERALISTS IN A FLUCTUATING LIGHT SPECTRUM

Maayke Stomp [1], Meike Wortel [1], Harriët M. J. Van Overzee [1], Mark A. Van Dijk [1], Martijn Egas [2], Jef Huisman [1]

[1] *University of Amsterdam, Institute for Biodiversity and Ecosystem Dynamics, Nieuwe Achtergracht 127, 1018WS, Amsterdam, The Netherlands*
[2] *University of Amsterdam, Institute for Biodiversity and Ecosystem Dynamics, Kruislaan 320, 1098SM, Amsterdam, The Netherlands*

egas@science.uva.nl

In this presentation, we report on experimental and theoretical tests of specialist-generalist coexistence under fluctuating conditions. Recent work has shown that green and red colored phytoplankton species of the *Synechococcus* complex coexist on white light by using different parts of the light spectrum (Stomp et al. Nature 2004). The pigment composition of these species is rather constant, and determines the color of light on which they are specialized: red light is absorbed with the green pigment phycocyanin, whereas green light is absorbed with the red pigment phycoerythrin. Other phytoplankton species can adapt their ratio of red and green pigments to the prevailing light spectrum, and hence they can be considered generalists. Previous work showed that such a generalist species can coexist on white light with either one of the specialist species by adapting its pigment composition to that part of the light spectrum that is not utilized by the specialist species. Here we examine, by theory and experiments, the possibility of coexistence between two specialists and a generalist under fluctuating red and green light conditions. We consider the impact of fluctuation frequency and adaptation rate of the generalist to the light conditions on coexistence of the three species in a mathematical model, and contrast the model predictions with results from competition experiments where the frequency of light fluctuations was varied.

09-09 Poster

THE EVOLUTION OF CO-EXISTING LEARNING AND NON-LEARNING FORAGING STRATEGIES

Sigrunn Eliassen [1], Marc Mangel [2], Jarl Giske [1]

[1] *University of Bergen, Department of Biology, PB 7800, N-5020, Bergen, Norway*
[2] *University of California, Department of Applied Mathematics and Statistics, CA95064, Santa Cruz, USA*

Sigrunn.Eliassen@bio.uib.no

In changing environments, foragers make apparently complex decisions on which prey to select, where to forage, and for how long to stay in a patch. The information that forms the basis for such decisions is obtained by exploring the environment and learning from experience, but these activities involve costs that may offset the advantage of a flexible response. The trade-off between a fixed strategy that specialises on specific conditions versus a flexible strategy that learns how to respond to environmental conditions may thus be understood as a generalist-specialist dilemma.

We use an individual-based genetic-algorithm model that explicitly considers behaviour and life-history traits. Movement and resource consumption by all individuals in a population determines competition and the spatial and temporal distribution of foragers and resources. The strategies are not predetermined, but evolve under the selective forces of the model environment. We then investigate how ecological factors such as offspring survival and predation on adults affect phenotypic diversification.

The results show that early in the season, high competition keeps resource levels stable, which facilitates fixed strategy foragers. Later in the season, flexible learning strategies prosper due to reduced competition and a more variable resource distribution. Strategies that differ in their learning ability thus proliferate during various parts of a foraging season. Coexistence between strategies are typically found when long foraging seasons allow for segregation of hatching times and when high forager densities intensify resource competition.

09-10 Poster

THE GENETIC CORRELATION BETWEEN DEVELOPMENT TIME AND ADULT BODY SIZE IS AFFECTED BY LARVAL FOOD AVAILABILITY IN A SCORPIONFLY.

Leif Engqvist [1]

[1] *University of Bonn, Department of Evolutionary Biology and Ecology, An der Immenburg 1, D-53121, Bonn, Germany*

lengqvist@evolution.uni-bonn.de

Development time and body size at maturation are two important fitness traits fundamental for our understanding of life history theory. Large body size is usually associated with high reproductive success, and individuals that develop fast will be able to start reproduce earlier. Yet, fast development is associated with small adult body mass, as it will take longer to grow large and this results in a trade-off between fast development and large body size. However, the strength of this trade-off may depend on environmental factors such as the average food availability, as the potential benefit of long development will depend on the rate of food intake. In the scorpionfly *Panorpa cognata* (Insecta, Mecoptera), there is considerable genetic variance for development time. Preliminary analyses of experiments made under diapause-free development have shown that at high larval food levels, long developing genotypes achieve larger body size. However when food is scarce, the sign of the genetic correlation changes, as genotypes with long development seem not be able to exploit and convert food resources into large body size as effectively as under conditions with ample food availability. Thus, there is a genotype-by-environment interaction suggesting that genotypes are differently adapted to various food levels during development. The relation between development time and body size may also be affected by the mode of development – whether diapause is induced or not. Initial analyses of experiments made under shorter light periods, inducing diapause, seem to reveal a somewhat different pattern.

09-11 Poster

EVOLUTIONARY ORIGINS OF A NOVEL HOSTPLANT DETOXIFICATION GENE IN BUTTERFLIES

Hanna M. Fischer [1], Christopher W. Wheat [2], David G. Heckel [1], Heiko Vogel [1]

[1] *MPI for Chemical Ecology, Entomology, Hans-Knöll-Str.8, 07745, Jena, Germany*
[2] *Pennsylvania State University, Biological Science, University Park, PA, 16802, USA*

hfischer@ice.mpg.de

The interactions between plants and their specialist insect herbivores provide an excellent opportunity to study the evolution of species interaction on a molecular level. Here we investigate the molecular evolutionary events that gave rise to a novel detoxifying enzyme (Nitrile-specifier Protein: NSP) in the butterfly family Pieridae. NSP redirects the hydrolysis of plant chemical defense glucosinolates to nitriles rather than toxic isothiocyanates in caterpillar guts, enabling them to feed on plants in the order Brassicales (Eurosid II, Dicotyledons). The appearance of NSP coincides with the emergence of the Brassicales family and was followed by significantly increased diversification rates identifying NSP as a key evolutionary innovation. We found NSP to be a member of an insect specific gene family we characterized and named NSP-related gene family. Members of this family consist of variable tandem repeats of a core domain, and can be found across insecta. The NSP-like gene family evolution is a dynamic, ongoing birth death process. By creating a robust phylogenetic analysis we show NSP and its orthologous gene to have a single evolutionary origin from an ancestral single domain gene. Genomic information and sequence identity analysis suggest evolution via both within and whole gene tandem duplication, during which both genes experienced a period of relaxed constraint followed by an increase of functional constraint attained after neofunctionalization. NSP and its ortholog are still subject to high rates of change, reflecting dynamic properties. We give new insights into the molecular evolutionary dynamics of an ecological important host shift and contribute evidence showing that within and whole gene tandem duplications are a powerful force driving evolutionary adaptation.

09-12 Poster

UNEXPECTED PATTERNS OF PLASTIC RESOURCE ALLOCATION IN STOCHASTIC ENVIRONMENTS

Barbara Fischer [1, 2], Barbara Taborsky [1, 2], Ulf Dieckmann [1]

[1] *International Institute for Applied Systems Analysis (IIASA),, Evolution and Ecology Program, Schlossplatz 1, A-2361, Laxenburg, Austria*
[2] *University of Bern, Department of Behavioural Ecology, Wohlenstrasse 50a, CH-3032, Hinterkappelen, Switzerland*

fischerb@iiasa.ac.at

In stochastic environments, individuals accrue fitness benefits by exhibiting phenotypic plasticity. Such benefits, however, are counterbalanced by costs of plasticity, which must be assumed to increase with the exhibited degree of plasticity. Here we introduce and analyze a general dynamic-programming model describing an individual's optimal resource allocation in a stochastic environment when plasticity is costly. At discrete moments after maturation, an individual decides repeatedly how to allocate available resources between maintenance and reproduction. We investigate the optimal fraction of resources invested into reproduction and the resultant degree of plasticity in dependence on the variability and predictability of the environment. Our analyses reveal unexpected patterns of optimal resource allocation. In environments with very low resource availability, the optimal allocation is to reproduction alone, although this implies that individuals will not survive after reproduction. Above a certain threshold of resource availability, the optimal reproductive investment decreases rapidly to a minimum, and will even vanish completely if the environment is highly unpredictable. With further improvement of resource availability, reproductive investment gradually increases again. These transitions in allocation strategies reflect how optimal solutions to the trade-off between current and future reproduction change with resource availability and are affected by environmental variability and predictability.

09-13 Poster

DIVERSIFICATION OF LONG WAVELENGTH-SENSITIVE VISUAL PIGMENTS IN BUTTERFLIES FOLLOWING HOST PLANT SHIFTS

Francesca D. Frentiu [1], Cristina I. Cuevas [1], Katy L. Prudic [2], Adriana D. Briscoe [1]

[1] University of California Irvine, Ecology and Evolutionary Biology, 321 Steinhaus Hall, 92697, Irvine, USA
[2] University of Arizona, Ecology and Evolutionary Biology, 85721, Tucson, USA

ffrentiu@uci.edu

Butterflies exhibit a remarkable diversity of visual pigment peak sensitivities (λ_{max}) in the long-wavelength (L; 500-600 nm) range, however the ecological reasons driving such diversification remain unknown. The butterfly genus *Limenitis* is ideal for investigating ecological correlates of this diversification because the mimetic North American species display a variety of L pigment peak sensitivities (λ_{max}=515-545 nm). We previously identified amino acid substitutions in the opsins coding for these pigments that may be responsible for spectral differentiation and showed these have been are under positive selection. Here we asked whether diversification of visual pigments occurred in tandem with the radiation of the North American species and mimicry-driven wing pattern diversification. We reconstructed phylogenetic relationships among European and North American *Limenitis* species using four genes and mapped the occurrence of amino acid substitutions implicated in spectral shifts. We found the majority of these substitutions occurred prior to the radiation of the North American species, but in tandem with a switch in larval host plants from honeysuckles to the tree family Salicacea. This switch is thought to have facilitated the colonization of the North American continent by an ancestral European *Limenitis* species and visual system diversification may have aided recognition of a potentially novel host plant.

09-14 Poster

EVOLUTION OF MIGRATION DISTANCE IN SHOREBIRDS

GABRIEL E. GARCÍA-PEÑA [1], GAVIN H. THOMAS [2], TAMÁS SZÉKELY [1], JOHN D. REYNOLDS [3]

[1] University of Bath, Department of Biology & Biochemistry, BA2 7AY, Bath, United Kingdom
[2] Imperial College of London, NERC Centre for Population Biology, SL5 7PY, Ascot, United Kingdom
[3] Simon Fraser University, Department of Biological Sciences, V5A 1S6, Burnaby, BC, Canada

gegp20@bath.ac.uk

One of the most spectacular animal behaviour is long-distance migration when many Arctic and temperate zone species leave their breeding grounds during winter, some of them travelling for thousands of kilometres to their winter refugees. Previous studies have provided valuable information on adaptations that allow birds to travel for long distances (e.g. energy use, orientation and synchronization). Here we investigate the evolution of migration distance following a less studied approach. We investigate how migration distance evolved in response to temperature at the breeding grounds and the length of the season; and how breeding systems constrain the evolution of migration distance. We test our hypotheses in shorebirds (sandpipers, plovers and allies), that exhibit one of the largest diversity among birds in both migratory behaviour and breeding systems (*e.g.* social monogamy, polyandry or polygyny). Using phylogenetic comparative analyses we found that migration distance decreases with minimum temperatures at breeding, the length of the breeding season and the provision of parental care by the male.

09-15 Poster

FROM PLASTICITY TO DIVERSITY: WHEN DEVELOPMENTAL PLASTICITY MIRRORS DIFFERENCES AMONG TAXA

Ivan Gomez-Mestre [1], Daniel R. Buchholz [2]

[1] Boston University, Biology, 5 Cummington St., 02215, Boston, USA
[2] University of Cincinnati, Biological Sciences, 832 Rieveschl Hall, 45221, Cincinnati, USA

igmestre@bu.edu

Developmental plasticity is found in most organisms, but its role in evolution remains controversial. Environmentally induced phenotypic differences may be translated into adaptive divergence among lineages experiencing different environmental conditions through genetic accommodation. To examine this evolutionary mechanism, we studied the relationship between plasticity in larval development, postmetamorphic morphology, and morphological diversity in spadefoot toads, a group of closely related species distributed throughout temperate areas of both the New and the Old World, that are highly divergent in larval period and body shape. Previous studies showed that accelerated metamorphosis is adaptive for desert dwelling spadefoot toads. We show that even under common garden conditions spadefoot toad species show divergent reaction norms for larval period. In addition, experimentally induced changes in larval period caused correlated morphological changes in postmetamorphic individuals such that long larval periods resulted in relatively longer hind limbs and snouts. A comparative analysis of morphological variation across spadefoot toad species also revealed a positive correlation between larval period and limb and snout lengths, mirroring the effects of within-species plasticity at a higher taxonomic level. Indeed, after ca. 110 Ma of independent evolution, differences in larval period explain 57% of the variance in relative limb length and 33% of snout length across species. Thus, morphological diversity across these species appears to have evolved as a correlated response to selection for reduced larval period in desert dwelling species, possibly diverging from ancestral plasticity through genetic accommodation.

09-16 Poster

HABITAT SPECIFIC DIFFERENTIATION IN THE FRESHWATER ISOPOD ASELLUS AQUATICUS – AN EXAMPLE OF PARALLEL EVOLUTION IN SHALLOW LAKES

Anders Hargeby [1], Nina Nowshiravani [2], Fabrice Eroukhmanoff [2], Erik Svensson [2]

[1] Linkoping University, IFM, Biology, SE-581 83 Linkoping, Sweden
[2] Lund University, Section for Animal Ecology, SE-223 62 Lund, Sweden

anhar@ifm.liu.se

Recent studies show that populations of the freshwater isopod *Asellus aquaticus* L. can be locally differentiated over a small geographic scale, even within lakes. Phenotypes are generally larger and darker in habitats structured by reed vegetation in habitats structured by submerged stonewort vegetation. To examine if this is a result of parallel evolution, we estimated genetic distance between isopods from the two types of habitats in four lakes, by means of molecular markers (AFLP and DNA sequence analysis). In two of the study lakes, we have previously noted contemporary differentiation in *Asellus* pigmentation as an adaptive evolutionary response to the establishment of stonewort vegetation. In the other two study lakes, the two contrasting habitat types have probably existed since the lakes became separated from the Baltic, approximately 4000 years ago. Because of these historical differences we also examined the heritability of *Asellus* pigmentation in individual populations. The results indicate that there is a strong genetic component in *Asellus* pigmentation ($h^2 = 0.9 - 1.0$), irrespectively of population history. The molecular analysis revealed that the genetic distance between habitats was small compared with genetic distance between lakes. This was consistent in lakes with recently differentiated populations, as well as in the two lakes with more ancient divergence. These results support the hypothesis that differentiation has occurred continuously in independent populations, and thus that the system is an example of parallel evolution.

09-17 Poster

LIFE ON THE EDGE: GENE FLOW IN RELATION TO DIFFERENT LIFE HISTORY STRATEGIES AND GEOGRAPHICAL DISTANCES IN TWO SPECIES OF MUD SNAILS IN THE BALTIC SEA.

Micaela A. Hellström-Phillips [1]

[1] *Åbo Academy University, Environmental and Marine Biology, Akademigatan 1, 20500, Åbo, Finland*

michells@abo.fi

Ecosystems that are geographically and ecologically marginal such as brackish waters are expected to show lower genetic diversity within populations and more different genotypes between populations than less extreme environments. The Baltic Sea is geologically young (8000 years) and brackish. It harbors populations which have evolved differently form the Atlantic populations showing divergences both due to bottlenecks and selection on adaptive traits.

The present study proposes to compare genetic connectivity and gene flow between populations of two species of mud snails in relation to reproductive strategies and geographical distances in the Baltic Sea by using different DNA markers. The two species selected for this study *Hydrobia ulvae* and *Hydrobia ventrosa* show direct and pelagic larval development stages respectively.

Genetic clines, dispersal and connectivity between the populations are discussed and comparisons with populations in the Atlantic will be made to determine genetic bottlenecks and local adaptation to the Baltic Sea.

09-18 Poster

RANK IN ANT ARMIES: HOW FATHERS INFLUENCE CASTE IN ARMY ANTS

Rodolfo Jaffé [1], Daniel J. C. Kronauer [2], F B. Kraus [3], Jacobus J. Boomsma [2], Robin F. A. Moritz [1]

[1] *Martin Luther University, Department of Biology, Hoher Weg 4, 06099, Halle, Germany*
[2] *University of Copenhagen, Department of Population Biology, Universitetsparken 15, 2100, Copenhagen, Denmark*
[3] *El Colegio de la Frontera Sur, ECOSUR, Carr. Antiguo Aeropuerto km 2.5, 30700, Tapachula, Mexico*

rodolfo.jaffe@zoologie.uni-halle.de

The ecological success of social insects is driven by the colony efficiency, characterized by a well organized division of labour among nest members. This requires a precise task allocation through the behavioural differentiation of individuals, which can be achieved either by behavioural or morphological specialization. In physical caste systems, the diet and rearing environment of developing larvae is known to determine the phenotype of adult individuals, although recent studies have shown that genetic components also contribute to the determination of worker caste polymorphism in simple caste systems. Here we show that even in army ants, which exhibit one of the most extreme worker polymorphism in social insects, gene effects determine worker caste fate. Worker size and function was found to vary among paternal subfamilies and hence was strongly determined by the genotype of the siring male. Since even in this highly complex multi-caste system genetic factors are an important driver for caste polymorphism, we conclude that it may well be a very basic and general principle to organize task specialization and division of labour in social hymenoptera. Additionally, in the line of previous works our results suggest that the combination of queen multiple mating and genetic variation for caste determination may have facilitated the evolution of worker caste diversity in some lineages of social insects.

09-19 Poster

STUDYING THE GENETIC BASIS OF HOST RANGE EXPANSION IN DIAMONDBACK MOTH PLUTELLA XYLOSTELLA L. (LEPIDOPTERA: PLUTELLIDAE)

Kathrin Janssen [1], Annette Reineke [2], Jan A. Scheirs [1], Astrid Groot [1], David G. Heckel [1]

[1] *Max Planck Institute for Chemical Ecology, Entomology, Hans Knoell Str. 8, 07745, Jena, Germany*
[2] *Forschungsanstalt Geisenheim, Phytomedicine, Von-Lade-Strasse 1, 65366, Geisenheim, Germany*

kjanssen@ice.mpg.de

Studying the genetic basis of host range expansion in herbivorous insects contributes to our understanding in adaptation to changing environments. The diamondback moth (DBM), *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), is a major pest on cruciferous plants throughout the world and its host range was thought to be restricted to Cruciferae until a recent record has indicated that a population in Kenya can survive on peas. This newly evolved pea host strain of DBM provides an excellent example for studying the underlying mechanisms of host plant adaptation in herbivorous (pest) insects.

To identify candidate genes associated with survivorship on peas we performed crosses to determine trait segregation and to generate a linkage map. The pea strain was hybridized with the crucifer strain, followed by crossing and backcrossing the F1 to both parental strains. Individuals were phenotyped for their ability to survive on pea. Survival rates of F1, F2 and BC offspring on pea suggest that one or more recessive genes are responsible for adaptation to pea. The same individuals were genotyped using AFLP markers. We obtained the expected 31 linkage groups (i.e. *P. xylostella* has 31 chromosomes) from > 200 female informative bands. Four linkage groups were found to be associated with the ability to survive on pea. Bands that identified these linkage groups could either be candidate genes or markers that are tightly linked to the ability to survive on peas. This work is a first step to construct a linkage map of DBM based on host adaptation and to explore the genetic basis of its recent host range expansion.

09-20 Poster

PHYLOGEOGRAPHY OF STURGEONS IN PONTO-CASPIAN REGION.

Nikolai Mugue [1], Anna Barmintseva [1], Sergei Rastorguev [1], Vladimir Barmintsev [1]

[1] *VNIRO, V. Krasnoselskaya str., 107140, Moscow, Russia*

mugue@mail.ru

Several sturgeon species have strong Ponto-Caspian distribution, inhabiting both Black/Azov-and Caspian Seas and rivers of these basins. Low genetic divergence between Azov and Caspian populations and high proportion of sheared haplotypes in beluga (Huso huso), stellate sturgeon (Asipencer stellatus), and Russian sturgeon (*A. gueldenstaedtii*) indicates recent migration events between two sea basins by Manych Stright. Two closely related species (*A. gueldenstaedtii* and Caspian endemic, *A. persicus*) share mtDNA haplotypes and taxonomic status of these two species has been questioned based on DNA analysis. Also, one group of mtDNA haplotypes, extremely similar to another distinct species, Siberian sturgeon (*A. baerii)* have been found abundant (appr. 30%) among *A. guldenstaedtii* caught in the Caspian Sea ("*baerii-like*" haplotypes by Birstein et al., 2000).

By sequencing mtDNA control region of over 500 samples of *A. gueldenstaedtii*, *A. persicus*, and *A. baerii*, we propose that presence of "*baerii-like*" haplotypes is a result of recent massive introgression of *A. baerii* from periglacial lakes discharged into the Caspian Sea. Introduced population of Siberian sturgeon underwent complete hybridization with Caspian population of Russian sturgeon. Absence of "*baerii-like*" haplotypes in the Black/Azov sea populations of *A. guldenstaedtii* can be explained by recent introduction of *A. baerii* in the Caspian basin (after closure of the Manych straight). Analysis of over 200 specimens of *A. persicus* has revealed no "*baerii-like*" haplotypes, which indicates that despite low genetic divergence, reproductive isolation has been established between *A. gueldenstaedtii* and *A. persicus* by the time of *A. baerii* invasion into the Caspian Sea.

09-21 Poster

ADAPTIVE SPECIATION IN TWO HABITATS

Jennie Nilsson [1], Jörgen Ripa [1]

[1] *Lund University, Theoretical Ecology, Ecology Building, 223 62, Lund, Sweden*

jennie.nilsson@teorekol.lu.se

We analyze a model of speciation in a system of two habitats, or islands, with discrete resources, connected by migration. We investigate the global, as well as the local, invasibility of this system.

We conclude that sympatric speciation in a system like this is unlikely. If the initially invading species has a narrow niche width, parapatric speciation can take place, resulting in one species on each island. After some divergence the two species will be able to invade the other island (secondary sympatry).

If the founding species has a broad niche, it may still speciate parapatrically, but secondary sympatry is hampered by a negative invasion fitness, i.e. one of the locally coexisting species is a sink population maintained by migrates from the other island. If the islands become isolated the sink population will not be able to persist.

In this single model we capture the processes of speciation, adaptive radiation, evolution in source-sink populations and secondary sympatry. It is a first step towards a more complete understanding of the process of adaptive radiation in heterogeneous environments.

09-22 Poster

SUFFLOGOBIUS BIBARBATUS - A SUCCESS SPECIES IN THE BENGUELA UP-WELLING SYSTEM DUE TO ITS TOLERANCE OF HYPOXIA AND HYDROGEN SULPHIDE.

Anne Gro V. Salvanes [1], Anna Bronwen Currie [2]

[1] *University of Bergen, Dept of biology, P.O.Box 7800, N-5020, Bergen, Norway*
[2] *Ministry of Fisheries, Aquaculture, NATmirc, P.O.Box 912, Swacobmund, Namibia*

anne.palm@bio.uib.no

The Benguela up-welling ecosystem (on the south-west cost of Africa) is one of the most productive areas of the world. Inner shelf has high sedimentation rate and large areas covered with hydrogen sulphide sediments, where anoxic or hypoxic conditions are found in the water column above. The endemic goby, *Sufflogobius bibarbatus* has shown to have grate success in this ecosystem. *S. bibarbatus,* is described as a pelagic goby. Or preliminary conclusion is that this goby is mostly in the pelagic to restore their oxygen depth and to digest, migrating up-words to more oxygenated water just after sunset and returning to low oxygen water just before sunrise to avoid predation.

Experimental studies showed that this goby has a remarkably high tolerance to low oxygen. Their respond to decreasing oxygen levels by an intermediate increase in the gill ventilation frequency followed by a sudden drop in gill beat frequency. They tolerate 5 hours in levels of < 0.01 ml DO/l without showing signs of equilibrium loss, and recover rapidly to normal breading and behaviour after 5 to 9 hours of oxygen stress. When "attacked" (poked by a stick) after been in < 0.01 ml DO/l for 5 hours, they responded immediately with an escape response, showing that their brain is turned on also after long time of anaerobe breading. Adult and juvenile gobies tolerated 5 hours in presence of H_2S in anoxic (< 0.01 ml DO/l) water without showing signs of equilibrium loss. We believe that this species remarkable tolerance to low oxygen - and high hydrogen sulphide levels is the explanation of its great success in the Benguela ecosystem.

09-23 Poster

RESOURCE-CONSUMER DYNAMICS OF BACTERIA LIVING ON DETRITUS RESOURCE

Minna H. Pekkonen [1], Jouni T. Laakso [1]

[1] *University of Helsinki, Department of Biological and Environmental Sciences, P.O.Box 65, Viikinkaari 1, 00014, Helsinki, Finland*

minna.pekkonen@helsinki.fi

The aquatic environment of bacteria contains not only nutrients but also growth inhibiting or enhancing substances that bacteria secrete. Therefore it is justified to assume that the interactions between individual bacterial cells are mediated largely by the growth medium. We have developed a simple method for measuring these interactions. We first filter-sterilize a sample of the growth medium where all species/strains have grown and then measure the instantaneous growth rate of each re-introduced species/strains in the filtrate to gain information on the quality of the environment experienced by the bacteria. We tested this method in a six day experiment with a community consisting of bacteria *Novosphingobium capsulatum* and *Serratia marcescens* feeding detritus resource. We found that the species compete for resources and also have temporally fluctuating asymmetric facilitation. In another 3.5 month experiment similar communities were grown in batch cultures and transferred weekly to a fresh growth medium. Live population samples were stored at each renewal time. The ancestral and evolved strains from this long term experiment were used to test adaptation to a complex resource environment. An analysis of evolutionary changes in species traits, resource-consumer interactions, and diversity is presented.

09-24 Poster

FROM PARTIAL TO DISJUNCT MIGRATION: HABITAT QUALITY OR COMPETITION?

Alvaro Ramírez [1], Javier Pérez-Tris [2], José Luis Tellería [3]

[1] *University of East Anglia, School of Biological Sciences, Centre for Ecology, Evolution and Conservation, NR4 7TJ, Norwich, United Kingdom*
[2] *Universidad Complutense, Facultad de Biología, Centre for Ecology, Evolution and Conservation, NR4 7TJ, Madrid, Spain*
[3] *Universidad Complutense, Facultad de Biología, Departamento de Zoología y Antropología Física, 28040, Madrid, Spain*

A.Ramirez@uea.ac.uk

Competition during winter with migratory conspecifics might have caused the extinction of populations breeding in the wintering range of many migratory birds, and hence the evolutionary transition from partial to disjunct migration. But other processes like the deterioration of breeding habitats in southernmost ranges, could also explain the evolution of disjunct migratory patterns. Our aim is to evaluate the relative role of environmental factors, geographical location or winter conspecific pressure in determining breeding range of two forest birds: robin *Erithacus rubecula* and blackcap *Sylvia atricapilla*. We used large-scale breeding distribution surveys, ringing recoveries of wintering birds, and environment remote sensing data available for 2,462 Spanish UTM squares (100 km^2). Results show that variables related to habitat quality, but not the abundance of wintering migrants, were strongly related to the distribution of resident breeding birds in both species. While residents breed in mature forests, migrants prefer to settle in other habitats that are very productive during winter, such as fruit-rich Mediterranean scrublands. This prevents any negative effect of migratory populations on Mediterranean breeding populations. Our results support the view that southern and marginal populations of robins and blackcaps are mainly restricted by the availability of suitable habitats. According to this, the withdrawal to north of forest optimum from Pleistocene times seems to be enough reason for explaining the distribution patterns of migratory and sedentary populations of these species.

09-25 Poster

SEXUAL REPRODUCTION PREVAILS IN A WORLD OF STRUCTURED RESOURCES IN SHORT SUPPLY

Barbara Drossel [1], Stefan Scheu [2]

[1] Darmstadt University of Technology, Institut fuer Festkoerperphysik, Darmstadt, Germany
[2] Darmstadt University of Technology, Institut fuer Zoologie, Darmstadt, Germany

scheu@bio.tu-darmstadt.de

We present a model for the maintenance of sexual reproduction based on the availability of resources, which is the strongest factor determining the growth of populations. The model compares completely asexual species to species that can switch between asexual and sexual reproduction. Key features of the model are that sexual reproduction sets in when resources become scarce, and that at a given place only a few genotypes can be present at the same time. We show that under a wide range of conditions the sexual species outcompete the asexual ones. The asexual species win only when survival conditions are harsh and death rates are high, or when resources are so little structured or consumer genotypes are so manifold that all resources are exploited to the same extent. These conditions in large represent when sexuals predominate over asexuals in the field.

09-26 Poster

ADAPTIVE FOOD WEB MODELS

Espen Strand [1], Frede Thingstad [1], Jarl Giske [1]

[1] University of Bergen, Department of Biology, Postboks 7800, N-5020, Bergen, Norway

Espen.Strand@bio.uib.no

An adaptive individual-based model of an idealized microbial food where two life-history traits, cell size and foraging mode, are simultaneously evolved is presented. The model is based on a genetic algorithm that mimics the processes of evolution by natural selection. Foraging (osmotrophy and phagotrophy) and mortality due to predation are modelled explicitly and thus contains density dependence. The most fit combinations (or niches) of cell size and foraging mode along continuous gradients emerge during a simulation. Several stable co-existing plankton functional types (PFTs) emerge with up to three trophic levels. Specialist competitors such as small-sized pure osmotrophs and larger pure phagotrophs emerge in all simulations. More generalist PFTs such as mixotrophic species emerge in some simulations depending on model parameter settings. The modeled habitat resembles a chemostat and variations in key parameters such as flow rate (i.e. background mortality) and nutrient concentration can significantly change the composition and diversity of the emergent functional types. The trophic length of the evolved food chain is very much influenced by the level of background mortality. Environmental parameters such as the concentration of dissolved nutrients is also an emergent property of the model and varies based on the composition and density of the PFTs.

The model also enables us to study population dynamics without evolution in adapted populations. Hopefully, such an approach will in the future enable usto include higher levels of complexity and hence more biological realism then previously possible.

09-27 Poster

DOES SPECIALIZATION DIFFER BETWEEN PLANT-POLLINATOR AND PLANT-HERBIVORE NETWORKS?

Elisa Thebault [1], Colin Fontaine [1]

[1] *NERC Centre for Population Biology, Imperial College London, Silwood Park Campus, SL5 7PY, Ascot, UK*

e.thebault@imperial.ac.uk

Mutualistic and trophic interactions are parts of the fundamental interactions that link species in natural communities and the concept of specialization has played a key role in the development of ecological and evolutionary understanding of both systems.

Recently, plant-pollinator networks have been found to be highly structured in a nested pattern which presents a continuum from specialist to highly generalist species and in which specialists interact with generalist species. This structure is often assumed to be particular to mutualistic interactions in opposition to the compartmentalized pattern expected for antagonistic networks with more specialised species. However, differences between mutualistic and antagonistic communities are still unclear due to the lack of direct comparison between these two types of networks and the use of different approaches.

We present here the results of a meta-analysis which compare 20 highly resolved plant – insect herbivore networks with 24 plant–pollinator networks. Our results indicate that these two types of networks differ both in the levels of insect generalism degree and in the frequency of asymmetric specialization. Our results offer promising perspectives for understanding the mechanisms that structure ecological communities.

09-28 Poster

ALTERNATIVE MATING TACTICS IN STICKLEBACKS: CAN EUTROPHICATION SHIFT THE ODDS?

Leon Vlieger [1], Ulrika Candolin [2]

[1] *University of Helsinki, Department of Biological and Environmental Sciences, Viikinkaari 1, P.O. Box 65, Helsinki, Finland*
[2] *Uppsala University, Department of Ecology and Evolution, Limnology, Husargatan 3, P.O. Box 573, Uppsala, Sweden*

leon.vlieger@helsinki.fi

Alternative mating tactics can arise whenever there is competition for a resource during reproduction. A common tactic in fish, for example sticklebacks, is sneak fertilisation. A male sneaks into a territory, intrudes on a courting couple and tries to mate with the female and fertilise her eggs before the resident male can do so. Visual cues are important here and environmental changes affecting visibility can thus have serious ramifications. Explosive blooms of algae as a consequence of human-induced eutrophication are changing underwater visibility in the Baltic Sea. My studies aim to determine how this affects sneaking behaviour in sticklebacks. This presentation will focus on the effects of changes in turbidity levels.

09-29 Poster

FAT-TAILED DISPERSAL ENABLES COLONISATION OF HUGE AREAS AND GIVES RISE TO A FRACTAL DISTRIBUTION OF GENOTYPES IN CLONAL ORGANISMS

Luzie U. Wingen [1], James K. M. Brown [1], Michael W. Shaw [2]

[1] *John Innes Centre, Disease and Stress Biology, Colney, NR4 7UH, Norwich, UK*
[2] *University of Reading, School of Biological Sciences, Whiteknights, RG7 6AS, Reading, UK*

luzie.wingen@bbsrc.ac.uk

Long-distance dispersal (LDD) plays an important role in many population processes like colonisation, range expansion and epidemics. LDD of small particles like fungal spores is often a result of turbulent wind-dispersal and is best described by functions with power-law behavior in the tails ('fat-tailed'). The influence of fat-tailed LDD on population genetic structure is not well understood. In computer simulations, the population structure generated by power-law dispersal with exponents in the range of -2 to -1 is distinctly different from that produced by exponential dispersal. Most importantly, the genotype distribution of power-law dispersed populations has a fractal structure. As the power-law exponent becomes smaller, the distribution of individual genotypes becomes more self-similar at different scales. Fractal and self-similarity statistics, some used in ecology and others developed here, demonstrated differences in structure arising from fat-tailed and exponential dispersal. In a large simulation arena, fat-tailed LDD allows colonisation of the entire space by all genotypes whereas exponentially bounded dispersal eventually confines all descendants of a single clonal lineage to a relatively small area. The influence of fat-tailed LDD on the population genetic structure in heterogeneous environments is currently under investigation.

Evolution of sex chromosomes

10

Saturday August 25 *Location*: Ekonomikum 3

Symposium 10: Evolution of sex chromosomes

ORGANIZERS: Dmitri Petrov, Stanford University, USA
Peter Arndt, Max Planck Institute for Molecular Genetics, Germany

14.00-14.30	**A. Bernardo Carvalho** (invited) Origin and evolution of the Y chromosome: Drosophila tales
14.30-15.00	**Doris Bachtrog** (invited) Y-chromosome degeneration and the evolution of dosage compensation
15.00-15.20	**Hans Ellegren** Rapid evolution of sex-linked genes in a female heterogametic system
15.20-15.50	*Coffee*
15.50-16.10	**John Baines** Adaptive evolution of X-linked and autosomal genes with sex-biased expression
16.10-16.30	**Kateryna Makova** What does it take to stay on sex chromosomes? The survival guide for genes
16.30-16.50	**Roberta Bergero** Evolutionary strata on the X chromosomes of the dioecious plant Silene latifolia: evidence from new sex-linked genes
16.50-17.10	**Dmitry Filatov** Mutagenic view of the sex chromosome evolution in Silene latifolia

10-01 Talk

ORIGIN AND EVOLUTION OF THE Y CHROMOSOME: DROSOPHILA TALES

A. Bernardo Carvalho [1], Andrew Clark [2], Leonardo Koerich [1]

[1] *Federal Univ. of Rio de Janeiro, Department of Genetics, Brazil*
[2] *Cornell University, Molecular Biology and Genetics, USA*

bernardo@biologia.ufrj.br

Y-chromosomes evolved independently many times and are a major biological phenomenon. Important questions about their origin and evolution remain unanswered, and *Drosophila* is a privileged model to study them. We highlight two of them. (i) Gene loss and gain are known to play an important role on the evolution of the Y. The recent sequencing of 12 *Drosophila* genomes allowed a detailed study of these processes. We previously showed that the *D. melanogaster* Y-linked genes were acquired from the autosomes. When we investigated the fate of 10 such genes in the additional *Drosophila* species, we found that the composition of the Y-chromosome is quite fluid: *FDY* is present only in the *D. melanogaster* Y, making it less than 3.5 Myr old. On the other hand, the arrival of *kl-2, kl-3, ORY, PRY* and *PPr-Y* onto the Y predates the split of the *Drosophila* and Sophophora subgenus (63 Myr ago). We also found intermediate cases: *WDY* is restricted to the Y of the melanogaster group, whereas *CCY* and *ARY* are Sophophora-specific. Our results identified a total of 4 gene gains and 2 gene losses from the Y on this phylogeny, and showed that the *Drosophila* Y is at least 63 Myr old, predating the split of all sequenced species. We are now studying the Y gene content of ~300 *Drosophila* species. (ii) Although it is certain that Y chromosomes usually arise from the degeneration of X chromo-somes, it remains an open point whether or not there are alternative pathways for the origin of the Y. The finding that none of the genes of the *D. melanogaster* Y are shared with the X is somewhat at odds with the hypothesis that the *Drosophila* Y was derived from the X. We found in 2005 that the ancestral Y of *Drosophila* became part of an autosome in *D. pseudoobscura*, and was replaced by a new construct of unknown origin. This finding has obvious implications for the origin and evolution of the Y, and raises the question of how frequent this phenomenon is. The ongoing study of 300 *Drosophila* Y will answer this question.

10-02 Talk

Y-CHROMOSOME DEGENERATION & THE EVOLUTON OF DOSAGE COMPENSATION

Doris Bachtrog [1]

[1] *University of California San Diego, Div. of Biological Sciences, 9500 Gilman Drive, 92093, La Jolla, USA*

dbachtrog@ucsd.edu

Ancient Y-chromosomes of various organisms show highly reduced levels of genetic activity and an abundance of repetitive DNA. In response, dosage compensation has evolved in many species with heterogametic sex chromosomes, to equalize expression levels of X-linked genes in males and females. The neo-Y chromosome of Drosophila miranda is in transition from an ordinary autosome to a genetically inert Y chromosome, while its homolog, the neo-X chromosome, is evolving partial dosage compensation. I will present DNA sequence and gene expression data of neo-sex linked genes in D. miranda, and link molecular degeneration of the neo-Y chromosome to the acquisition of dosage compensation on the neo-X.

10-03 Talk

RAPID EVOLUTION OF SEX-LINKED GENES IN A FEMALE HETEROGAMETIC SYSTEM

Judith Mank [1], Erik Axelsson [1], Martin Zwahlén [1], Hans Ellegren [1]

[1] *Uppsala University, Dept of Evolutionary Biology, Norbyvägen 18D, SE-752 36, Uppsala, Sweden*

Hans.Ellegren@ebc.uu.se

Theoretical work predicts natural selection to be more efficient in the fixation of beneficial mutations in X-linked genes than in autosomal genes. This "fast-X effect" should be evident by an increased ratio of non-synonymous to synonymous substitutions (dN/dS) for sex-linked genes; however, recent studies have produced mixed support for this expectation. To make an independent test of the idea of fast-X evolution we focused on birds which have female heterogamety (males ZZ, females ZW), where analogous arguments would predict a fast-Z effect. 2.8 Mb of orthologous protein-coding sequence of zebra finch and chicken, from 172 Z-linked and 4,848 autosomal genes were aligned. Zebra finch data were in the form of EST sequences from brain cDNA libraries while chicken genes were from the draft genome sequence. The dN/dS ratio was significantly higher for Z-linked (0.110) than for all autosomal genes (0.085; $p<0.001$), as well as for genes linked to similarly sized autosomes 1-10 (0.0948, $p=0.011$). This pattern of fast-Z was evident even after we accounted for the non-random distribution of male-biased genes. We also examined the nature of standing variation in the chicken protein-coding regions. The ratio of non-synonymous to synonymous polymorphism (pN/pS) did not differ significantly between genes on the Z chromosome (0.104) and on the autosomes (0.0917). In conjunction, these results suggest that evolution proceeds more quickly on the Z chromosome, where hemizygous exposure of beneficial non-dominant mutations increases the rate of fixation.

10-04 Talk

ADAPTIVE EVOLUTION OF X-LINKED AND AUTOSOMAL GENES WITH SEX-BIASED EXPRESSION

John F. Baines [1], John Parsch [1]

[1] *LMU Munich, Section of Evolutionary Biology, Grosshaderner Str. 2, 82152, Planegg-Martinsried, Germany*

baines@zi.biologie.uni-muenchen.de

Many genes in higher eukaryotes show sexually dimorphic expression, and these genes tend to be among the most divergent between species. In most cases, however, it is not known whether this rapid divergence is caused by positive selection, or if it is due to a relaxation of selective constraint. To determine the type and strength of selection affecting the evolution of sex-biased genes, we investigated DNA sequence polymorphism and divergence in 136 Drosophila melanogaster genes with male-, female-, or nonsex-biased expression. Our sample also included X-linked and autosomal genes from each expression category. Overall, we find the strongest signal of adaptive evolution for male-biased genes, especially those that are X-linked. We also find evidence for adaptive evolution of both X-linked and autosomal female-biased genes. Nonsex-biased genes, in contrast, show little sign of adaptive evolution. These observations suggest that recessive male-beneficial mutations contribute to the increased frequency of positive selection among male-biased genes on the X chromosome and offer further evidence that sexual selection and intersexual co-evolution are major forces driving genetic differentiation between species.

10-05 Talk

WHAT DOES IT TAKE TO STAY ON SEX CHROMOSOMES? THE SURVIVAL GUIDE FOR GENES

Kateryna D. Makova [1], Melissa Wilson [1]

[1] *Penn State University, Department of Biology, 208 Mueller Lab, PSU, 16802, University Park, PA, USA*

kdm16@psu.edu

The mammalian sex chromosomes, X and Y, evolved from a pair of homologous autosomes. However, the gene content differs between the two sex chromosomes; the X chromosome has many genes and its gene content is conserved among mammals, while the Y chromosome has few genes and its gene content might be variable among mammals. To tackle the causes of these differences, we investigate genes located in the X and the Y added regions (XAR and YAR) that were translocated to the sex chromosomes in eutherian mammals (e.g., humans and mice) after their divergence from marsupials (e.g., opossum) and monotremes (e.g., platypus). Since the time of translocation, genes in the XAR and YAR have been evolving as sex-linked genes in eutherian mammals, but as autosomal genes in both marsupial and monotreme mammals, and so allow for direct investigation of how sex-linkage alters the evolutionary path of a gene. We analyze the evolution of all XAR genes with Y-linked gametologues in mouse and human (or just in human) and compare them with their autosomal counterparts in opossum and platypus. The ratio of nonsynonymous to synonymous substitution rates is low on the X-specific branches. In contrast, Y-specific branches exhibit one of the two patterns: either high conservation or high divergence. These patterns are then correlated with expression differences between the X and Y gene copies in both human and mouse. Taken together, expression divergence and sequence evolution help elucidate mechanisms of gene retention on the sex chromosomes.

10-06 Talk

EVOLUTIONARY STRATA ON THE X CHROMOSOMES OF THE DIOECIOUS PLANT SILENE LATIFOLIA: EVIDENCE FROM NEW SEX-LINKED GENES

Roberta Bergero [1], Deborah Charlesworth [1]

[1] *University of Edinburgh, Institute of Evolutionary Biology, Edinburgh, UK*

r.bergero@ed.ac.uk

Sex-chromosomes of mammals and birds show signs of progressive suppression of recombination having created evolutionary strata of different X-Y divergence. Previous studies on the young sex-chromosome system of the plant Silene latifolia have also suggested the presence of evolutionary strata, despite their recent evolutionary origin, although such evidences were based on few sex-linked gene sequences. More genes are therefore needed. Here, by segregation analysis of intron size-variants ("ISVS") and single nucleotide polymorphisms (SNPs) we identify four new Y-linked genes one being duplicated on the Y chromosome, and test for evolutionary strata. All the new genes have homologues on the X and Y chromosomes. Synonymous site divergence (Ks) values estimated between the X and Y homologue pairs are within the range of those already reported, thus indicating that the divergence value is saturated, and confirming the cessation of X-Y recombination in the evolution of the sex chromosomes at about 10-20 MYA. The new X-linked loci were genetically mapped and a strict correlation was found between divergence from the homologous Y loci and genetic distance from the pseudo-autosomal region. Two distinctly separated clusters of X/Y divergence values were observed, thus suggesting that the sex-chromosome evolution in this plant species was accompanied by at least two events of recombination suppression. Ongoing studies will relate these events to the evolutionary transition from hermaphroditism to gynodioecy and finally dioecy.

10-07 Talk

MULIGENIC VIEW OF THE SEX CHROMOSOME EVOLUTION IN SILENE LATIFOLIA

Dmitry Filatov [1], Andrea Harper [1], Graham Muir [1]

[1] *University of Birmingham, School of Biosciences, Edgbaston, Birmingham B15 2TT, United Kingdom*

d.filatov@bham.ac.uk

Most species in the plant genus *Silene* (*Caryophyllaceae*) are non-dioecious, and dioecy (i.e. separate male and female individuals) and sex chromosomes have evolved in a small cluster of species (section *Elisanthe*). The best studied species, *S. latifolia*, is estimated to have diverged from a non-dioecious ancestor 10-20 million years ago providing an excellent opportunity to study the early stages of sex chromosome evolution. Evolutionary theory predicts that the lack of recombination on the Y chromosome should result in a substantial reduction of genetic diversity in Y-linked genes due to processes such as background selection and selective sweeps. It was previously demonstrated that DNA diversity in the *S. latifolia* Y chromosome is indeed drastically lower than in the X-linked genes. However, the comparisons with other genomic compartments are still missing. Here we report comparisons of DNA polymorphism in five pairs of *S. latifolia* sex-linked genes and 20 unlinked autosomal loci. Surprisingly, the autosomal loci in *S. latifolia* are less polymorphic, compared to X-linked loci, which is contrary to what is expected from their ploidy. Thus, previous comparisons of the level of polymorphism on the *S. latifolia* X and Y chromosomes may have overestimated the reduction of DNA diversity for the Y chromosome in this species. The reasons for the higher DNA diversity in the X chromosome, compared to autosomes and implications of this finding to our understanding of Y chromosome evolution are discussed.

10-01 Poster

INFERRING SELECTION FROM TRANSPOSON INTERRUPTIONS ON THE X CHROMOSOME

Gyorgy Abrusan [1], Joti Giordano [1], Peter E. Warburton [1]

[1] *Mount Sinai School of Medicine, Department of Genetics and Genomic Sciences, 1425 Madison Ave, 10029, New York, NY, USA*

gyorgy.abrusan@mssm.edu

In mammals, females must compensate for their double amount of X-linked genes (compared to males), which is achieved by the inactivation of one of the two X-chromosomes. It has been hypothesised that L1 transposable elements enhance the spread of inactivation signal along the chromosome, and the high density of L1s near inactivated genes has been interpreted in support of their functionality. However, at present there is no evidence that the accumulation of L1s on the X chromosome is indeed a cause and not the consequence of X inactivation. We tested the possible selective advantage of L1 families with a novel method, interruption analysis. In mammalian genomes a large number of transposable elements (TEs) interrupt other TEs, due to their high abundance. Such interruptions can be used to test whether TEs are selectively neutral, because functional TE copies are likely to be interrupted less frequently than non-functional ones. We tested whether the pattern of interruptions of L1s on the X chromosome is different from the autosomes. Our results support the hypothesis that L1 are functional; L1 elements of the oldest evolutionary strata of the X chromosome, which contain the highest density of the inactivated genes, are significantly less frequently interrupted than on the autosomes.

10-02 Poster

SEX-LINKED DIFFERENTIATION BETWEEN INCIPIENT SPECIES OF WOOD-WARBLER

Alan T. Brelsford [1], Darren Irwin [1]

[1] *University of British Columbia, Zoology Dept, 6270 University Blvd, V6T1Z4, Vancouver, BC, Canada*

alanb@zoology.ubc.ca

The role of sex chromosomes in speciation has received increasing theoretical and empirical support, but few cases have been documented in birds. Here, we present data on polymorphism and differentiation of twelve nuclear loci in two parapatric subspecies of Yellow-rumped Warbler (*Dendroica coronata*). One sex-linked and one autosomal site show reduced variation within subspecies and fixed differences between subspecies, suggesting linkage to loci that have evolved separately under selection. Despite the abundance of hybrids in the contact zone, linkage disequilibrium between these markers indicates that gene flow between populations is reduced, at least at these two loci. The genomic region of low variation on the Z chromosome extends at least 3 MB around the CHD1Z gene, which is located adjacent to the centromere in another passerine bird, the Zebra Finch. These results offer evidence of the importance of sex chromosomes and genomic regions of reduced recombination for speciation in the face of gene flow.

10-03 Poster

SEX CHROMOSOMES IN THE BASIDIOMYCETE FUNGUS MICROBOTRYUM

Benjamin Devier [1], Tatiana Giraud [1], Micheal E. Hood [2], Jessie Abbate [3], Roxana Yockteng [4]

[1] *Université de Paris-Sud, Ecologie, Systématique et Evolution, 15 rue Georges Clemenceau-Batiment 360, 91405, Orsay, France*
[2] *Amherst College, Biology Department, Amherst College Rts 9 & 116, 01002-5000, Amherst, USA*
[3] *University of Virginia, Department of Biology, Gilmer 051, VA 22903, Charlottesville, USA*
[4] *CNRS-MNHN, Systématique et Evolution, 16 rue Buffon, 75005, Paris, France*

benjamin.devier@u-psud.fr

The origin of sex chromosomes remains a central challenge in evolutionary genetics. Dimorphic sex chromosomes have evolved independently in diverse groups of animals, plants, and even fungi from ancestral autosome pairs. Sex chromosome dimorphism evolves because of recombination suppression and in several plants and animals, "evolutionary strata" have been found. The most plausible model for the recombination suppression is the selection for linkage around an original sex determination region. In fungi, the sex-determining region is the mating type locus and suppression of recombination occurs around it in some species. In basidiomycete fungi, mating types are composed of two loci. Tetrapolar systems have thousands mating types and the two loci are unlinked. Bipolar systems have two mating types and most often the two loci are linked.

Microbotryum violaceum is a bipolar basidiomycete, causing the anther-smut disease on caryophyllaceae species. Dimorphic sex chromosomes exist in several *Microbotryum* species. We isolated two pheromone receptors in EST libraries of *Microbotryum* species, corresponding to the A1 and A2 mating types. We performed phylogenies of its and of a linked DNA fragment in 27 Microbotryum species. The comparison of these phylogenies shows that there are at least two “evolutionary strata” on the *Mycrobotryum* sex chromosomes and that they occurred independently multiple times.

10-04 Poster

SEX CHROMOSOMES AND REPRODUCTION IN THE FREE-LIVING GENERATION OF THE PARASITIC NEMATODE STRONGYLOIDES PAPILLOSUS

Alexander G. Eberhardt [1], Linda Nemetschke [1], Werner E. Mayer [1], Adrian Streit [1]

[1] *Max Planck Institute for Developmental Biology, Evolutionary Biology, Spemannstr. 37-39, 72076, Tuebingen, Germany*

alexander.eberhardt@tuebingen.mpg.de

The nematode *Strongyloides papillosus* is a common intestinal parasite of ruminants. The parthenogenetic, parasitic female produces eggs that either develop directly into infective larvae that are all female or into the females and males of a facultative free-living generation. Different species in the genus *Strongyloides* differ in their chromosome number and sex determining systems. Some have two autosomes and one X-chromosome (2N=6) and employ an XX/X0-system for sex determination while for others only two chromosomes and no caryotypic difference between the sexes have been described. The later has been proposed to represent an evolutionary loss of a sex chromosome. *S. papillosus* appears to be a special, probably intermediate, case in that females have two pairs of chromosomes, while males have five chromosomes as a result of a sex specific chromatin diminution event that eliminates an internal portion of one chromosome. Based on cytological studies it was proposed for several *Strongyloides* species, including *S. papillosus*, that the males do not contribute genetic material to the offspring but are merely required to initiate parthenogentic development of the egg. It is difficult to imagine that this pseudogamy with the cost of maintaining males but without the advantages of sexual recombination should be evolutionary stable. By using molecular genetic markers we could show that *S. papillosus* males do contribute genetically to the progeny in most if not all cases, as it had already been shown for *S. ratti*. Interestingly, some markers are passed on to the offspring in a manner that is consistent with standard, mendelian, autosomal inheritance while for others males pass on preferentially or exclusively only one of their alleles. We are testing the hypothesis that this is the consequence of the particular sex determining system of *S. papillosus*.

10-05 Poster

X CHROMOSOME INACTIVATION DURING DROSOPHILA SPERMATOGENESIS

Winfried K. Hense [1], John F. Baines [1], John Parsch [1]

[1] *University of Munich, Department Biology II, Section of Evolutionary Biology, Grosshaderner Strasse 2, 82152, Planegg-Martinsried, Germany*

hense@zi.biologie.uni-muenchen.de

Genes with male- and testis-enriched expression are underrepresented on the Drosophila melanogaster X chromosome. There is also an excess of retrotransposed genes, many of which are expressed in testis, that have "escaped" the X chromosome and moved to the autosomes. It has been proposed that early inactivation of the X chromosome during spermatogenesis contributes to these patterns: genes with a beneficial function late in spermatogenesis should be selectively favored to be autosomal in order to avoid inactivation. However, conclusive evidence for early X inactivation has been lacking. To test if such inactivation occurs, we used a transgenic construct in which expression of a lacZ reporter gene was driven by the promoter sequence of the autosomal, testis-specific ocnus gene. Autosomal insertions of this transgene showed the expected pattern of male- and testis-specific expression. X-linked insertions, in contrast, showed little or no reporter gene expression. Thus, we find that X-linkage inhibits the activity of a testis-specific promoter. We obtained the same result using a vector in which the transgene was flanked by chromosomal insulator sequences. These results are consistent with global inactivation of the X chromosome and support a selective explanation for X chromosome avoidance of genes with beneficial effects late in spermatogenesis.

10-06 Poster

ANALYSIS OF THE X/Y RECOMBINATION ARREST: LESSONS FROM THE STUDIES ON XYY PLANTS IN SILENE LATIFOLIA

Bohuslav Janousek [1], Michaela Markova [1], Jitka Zluvova [1], Francoise Moneger [2], Ioan Negrutiu [2], Boris Vyskot [1]

[1] Institute of Biophysics, Department of Plant Developmental Genetics, Kralovopolska 135, CZ-612 65, Brno, Czech Republic
[2] Université de Lyon, ENS Lyon, Laboratoire RDP, IFR128 BioSciences Lyon-Gerland, 693 64, Lyon, France

janousek@ibp.cz

Theories on sex chromosome evolution predict that primary sex determining regions are small, but various evolutionary processes working on the Y-chromosome result in a stepwise arrest of recombination in surroundings of the primary sex determining region. One of the widely discussed mechanisms of the recombination arrest are chromosomal rearrangements (especially chromosomal inversions). Another possibilities are represented by genes modulating recombination ability of certain regions, and by changes in recombination hot-spots located on the Y-chromosome.

Here we present an artificially constructed model system for the study of the recombination ability of the Y-chromosome in the model dioecious species *Silene latifolia* (white campion). This experimental system enables to the Y-chromosomes coming from different populations to pair and recombine. Using the multiple molecular markers we have studied segregation of various parts of the Y-chromosomes in the progeny of the XYY plant heterozygous for Y-linked markers. Our results support the view that chromosome rearrangements do not represent the only mechanism of the recombination arrest between the X-and Y-chromosomes.

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10-07 Poster

EVOLUTION OF THE MATING-TYPE CHROMOSOME IN THE FILAMENTOUS ASCOMYCETE NEUROSPORA TETRASPERMA – IMPLICATIONS FOR SEX CHROMOSOME EVOLUTION

Audrius Menkis [1], David J. Jacobson [2], Hanna Johannesson [1]

[1] Uppsala university, Department of Evolutionary Biology, Norbyvägen 18D, 752 36, Uppsala, Sweden
[2] Stanford University, Department of Biological Sciences, 5020, CA 94305, Stanford, USA

hanna.johannesson@ebc.uu.se

Fungi with bipolar mating-systems, such as filamentous ascomycetes, exists as two alternative mating types whose cells fate are governed by a single chromosomal locus with two alleles. In the self-fertile species *Neurospora tetrasperma* recombination is blocked for 60 % of the mating-type chromosome. This is to accomplish packaging of two haploid nuclei of opposite mating-type into each of the four ascospores. Although the mechanism initiating the divergence of mating-type chromosomes differ from that of animal and plant sex chromosomes, the mating-type chromosome of *N. tetrasperma* resemble the sex chromosomes in failing to recombine over most of its length.

We revealed gene order on the *N. tetrasperma* mating-type chromosome by introgressing each of its mating-type chromosomes into a genetic background of its outcrossing close relative *N. crassa*, and performed fine tuned genetic mapping. In order to reconstruct any sequential evolutionary events fashioning the large region of the mat-chromosome with suppressed recombination, we compared the genealogies of the genes in the block between lineages of *N. tetrasperma*, and also compared the synonymous substitution divergence between parts of the mating-type chromosomes of one strain. Using both of these approaches, we confirmed that recombination ceases over the majority of the suppressed region during a short time interval, most probably at the time of divergence from its outcrossing ancestor, *N. crassa*.

10-08 Poster

TOWARDS A MECHANISTIC EVOLUTIONARY THEORY OF SEX DETERMINATION: THE IMPORTANCE OF SELECTION AGAINST INTERSEXES.

Magdalena Kozielska [1, 2], Andries Van der Meer [2, 3], Leo W. Beukeboom [1], Franz J. Weissing [2], Ido Pen [2]

[1] *University of Groningen, Evolutionary Genetics, Kerklaan 30, 9751 NN, Haren, The Netherlands*
[2] *University of Groningen, Theoretical Biology, Kerklaan 30, 9751 NN, Haren, The Netherlands*
[3] *University of Twente, Polymer Chemistry and Biomaterials, P.O.Box 217, 7500 AE, Enschede, The Netherlands*

m.a.kozielska@rug.nl

We present a mechanistic model for the evolution of sex determining systems based on recent insights from molecular studies. Specifically, we use individual-based simulations to model the gradual evolution of regulatory genes with a quantitative effect on the amount of a feminizing product. The amount of product must surpass a noisy threshold level to trigger female development, otherwise males are produced, or sterile intersexes if the amount of product is too close to the threshold. We impose sex ratio selection by assuming cost differences in the production of sons and daughters. By letting both maternal genes and offspring genes affect the level of feminizing product in the developing offspring, maternal-offspring sex ratio conflict drives the evolution of the regulatory genes. Selection against intersexes leads to dimorphism of either offspring genes or maternal genes, but not both. When a dimorphism evolves in offspring genes, either a female-heterogametic or a male-heterogametic sex determining system is the outcome, and the sex ratio stabilizes at equality. By contrast, when maternal genes evolve to a dimorphic state, monogeny evolves; that is, all females produce single-sex families, and the population sex ratio evolves to the maternal optimum. Which system evolves is to some extent random but can be partially predicted by initial conditions and the direction and strength of sex ratio selection. Thus, selection against intersexes combined with the maternal-offspring conflict over sex ratio can lead to the evolution of the main sex determining systems seen in nature.

10-09 Poster

PHYLOGENY OF SEX-DETERMINING MECHANISMS IN SQUAMATE REPTILES: ARE SEX CHROMOSOMES AN EVOLUTIONARY TRAP?

Martina Pokorna [1], Kratochvil Lukas [2]

[1] *Charles University, Zoology, Vinicna 7, 128 44, Prague, Czech Republic*
[2] *Charles University, Ecology, Vinicna 7, 128 44, Prague, Czech Republic*

lukkrat@email.cz

The gender of squamate reptiles is determined either by genotypic sex determination (GSD), where sex of an individual is determined by sex chromosomes, or by temperature-dependent sex determination (TSD), where sex chromosomes are lacking and sex is determined entirely by environmental factors. After gathering information about sex-determining mechanisms for more than 400 species, we employed comparative phylogenetic analysis using the maximum parsimony method to reconstruct the evolution of sex determination in Squamata. Our results suggest relative uniformity in sex-determining mechanisms in the majority of the squamate lineages. Well-documented variability is found only in dragon lizards (Agamidae) and geckos (Gekkota). Polarity of the sex-determining mechanisms in outgroups identified TSD as the ancestral mode for Squamata. Based on the classical phylogenetic hypothesis, transitions were strictly unidirectional from TSD to GSD. Using the molecular tree, one putative transition from GSD to TSD, namely in agamids, was exposed, but even in this case, the eleven (or more) transitions from TSD to GSD were much more frequent. We postulate that the evolution of sex-determining mechanisms in Squamata was restricted to the transitions from ancestral TSD to GSD. In other words, transitions were from the absence of sex chromosomes to the emergence of sex chromosomes, which have never disappeared and constitute an evolutionary trap. This evolutionary trap hypothesis changes the understanding of phylogenetic conservatism of sex-determining systems in many large clades such as butterflies, snakes, birds, and mammals.

10-10 Poster

THE IMPORTANCE OF POPULATION STRUCTURE FOR THE EVOLUTION OF HAPLODIPLOIDY

Bram Kuijper [1], Laura Ross [1], Ido R. Pen [1]

[1] *University of Groningen, Theoretical Biology, PO Box 14, NL9750 AA Haren, Haren, the Netherlands*

a.l.w.kuijper@rug.nl

In haplodiploid species, males exclusively transmit the maternally derived part of their genome. Haplodiploidy has originated at least 20 times across various invertebrate phyla, and several different hypotheses have been proposed to account for its evolution. Recent comparative analyses indicate an association between haplodiploidy, maternally transmitted endosymbionts and high levels of kin competition. This has sparked a number of models exploring the role of these factors in the evolution of haplodiploidy. However, these models did not take into account the potential importance of geographic population structure, which may strongly affect kin competition and inbreeding. We present the results of individual based models showing that population structure has a strong impact on endosymbiont-induced evolution of haplodiploidy.

10-11 Poster

EVOLUTION@HOME: GLOBAL COMPUTING QUANTIFIES EVOLUTION DUE TO MULLER'S RATCHET

Laurence Loewe [1]

[1] *University of Edinburgh, Institute of Evolutionary Biology - School of Biological Sciences, Ashworth Laboratories - Kings Buildings - West Mains Road - Edinburgh EH9 3JT, Scotland UK*

Laurence.Loewe@ed.ac.uk

The observation of high mitochondrial mutation rates in human pedigrees has led to the question of how such an asexual genetic system can survive the accumulation of slightly deleterious mutations caused by Muller's ratchet. I define a null model to quantify in unprecedented detail the threat from extinction caused by Muller's ratchet. This model is general enough to explore the biological significance of Muller's ratchet in various species where its operation has been suspected. For increased precision over a wide range of parameter space I employ individual-based simulations run by evolution@home, the first global computing system for evolutionary biology. After compiling realistic values for the key parameters in human mtDNA I find that a surprisingly large range of biologically realistic parameter combinations would lead to the extinction of the human line over a period of 20 million years - if accepted wisdom about mtDNA and Muller's ratchet is correct. The resulting genomic decay paradox complements a similar threat from extinction due to mutation accumulation in nuclear DNA and suggests evaluation of unconventional explanations for long-term persistence. A substantial list of potential solutions is given, including compensatory back mutations, mutation rate heterogeneity and occasional recombination in mtDNA. Future work will have to explore, which of these actually solves the paradox. Similar processes are expected to influence the role of Muller's ratchet in the evolution of sex chromosomes.

10-12 Poster

SEX REVERSALS IN THE COMMON FROG, RANA TEMPORARIA?

Chikako Matsuba [1], Ikuo Miura [2], Juha Merilä [1]

[1] University of Helsinki, Biological and Environmental Sciences, Viikinkaari 1, Biokeskus 3, FIN-00014, Helsinki, Finland
[2] Hiroshima University, Institute for Amphibian Biology, 1-3-1, Kagamiyama, Higashi-Hiroshimashi, 739-8526, Hiroshima, Japan

chikako.matsuba@helsinki.fi

Understanding of sex ratio dynamics in a given species requires understanding its sex determination system, as well as access for reliable tools for sex identification at different life stages. As in the case of many other amphibians, the common frogs (Rana temporaria) do not have well differentiated sex chromosomes, and identification of individuals' genetic sex may be complicated by sex reversals. To explore the sex determination system of the common frog, we screened microsatellite markers for sex-linkage using wild collected individuals and laboratory reared full-sib families. A strong linkage between sex and one marker was found in four geographically disparate populations, suggesting male heterogamy in common frogs. However, this linkage was absent in several other populations. Comparison of inheritance patterns of alleles and phenotypic sex within sibships revealed a mixed evidence for sex linkage: all individuals with male phenotype carried a male specific allele in one population, whereas results were more mixed in another population. Results suggest the genetic sex determination system in common frogs is male heterogamy, but sex reversals may be common.

10-13 Poster

THE PHYLOGENY OF NEUROSPORA (ASCOMYCOTA) AND THE POSSIBILITY OF MULTIPLE ORIGINS OF SELF-COMPATIBILITY IN THE GENUS

Kristiina Nygren [1], Tim Gustafsson [1], Hanna Johannesson [1]

[1] Uppsala University, Evolutionary Biology Centre, Sweden

kristiina.nygren@ebc.uu.se

The genus *Neurospora* contains species representing the major sexual modes found in the Ascomycetes; obligate outcrossing (heterothallic), selfing (homothallic) and intermediates (pseudohomothallic). Sexual compatibility is determined by the mating type locus which can be either *A* or *a*. In outcrossing species each individual can mate only with an individual of the other mating type. However, occasional overcrossing events in the mating type locus have the potential to construct a genome containing both mating types which leads to a self-compatible strain. The selfing lineages of *Neurospora* show a variety in their genetic composition of the mating type region indicating that they might be the result of several independent overcrossing events.

Further, it is debated whether the genus *Gelasinospora* is actually distinct from *Neurospora* or whether the two genera should be merged together. It is therefore needed to construct a robust phylogeny containing both genera.

Here we present a phylogeny based on partial sequences from four genes (β-tubulin, elongation factor 1-α, protein kinase C and 28S rDNA) from 44 taxa, representing most species of *Neurospora* and *Gelasinospora*. The phylogeny is used to test whether selfing lineages form a monophyletic group as well as to test for the monophyly of *Gelasinospora* and *Neurospora*.

10-14 Poster

SEARCHING FOR SEX CHROMOSOMES IN EYELID GECKOS (SQUAMATA: EUBLEPHARIDAE), A GROUP WITH CONTRASTING SEX-DETERMINING SYSTEMS. I. CONVENTIONAL KARYOTYPES OF TSD AND GSD SPECIES

Martina Pokorná [1], Lukáš Kratochvíl [1], Marie Rábová [2]

[1] *Charles University, Viničná 7, 12844, Praha, Czech Republic*
[2] *Academy of Sciences of the Czech Republic, Rumburská 89, 27721, Liběchov, Czech Republic*

pokornam@centrum.cz

In reptiles, sex determination occurs basically in two different modes: the sex of an individual is set either by its genotype (genotypic sex determination, GSD), or by environmental factors such as temperature during incubation (temperaturedependent sex determination, TSD). Although sex ratios can also be shaped by environmental factors in the case of GSD, the basic dichotomy between GSD and TSD is the presence/absence of sex chromosomes. In many species, GSD was determined solely by the observation of equal sex ratios at several incubation temperatures; cytogenetic methods necessary for identification of sex chromosomes have not been applied yet. Eyelid geckos represent an interesting system for exploring the phylogeny and evolution of sex-determining mechanisms in general, and sex chromosomes in particular. This clade includes two TSD species (*Eublepharis macularius,Hemitheconyx caudicinctus*). In *Coleonyx elegans*, *C. mitratus, Goniurosaurus luii* and *G. lichtenfelderi* we observed equal sex ratios at all examined incubation temperatures, which was described earlier in *C. variegatus*. Therefore, we concluded that these species possess GSD. Next, we compared karyotypes of both sexes in all mentioned TSD and GSD species and searched for the presence of heteromorphic sex chromosomes. Using conventional staining, we have not found sexual differences in karyotypes of any species. This suggests that sex chromosomes in examined GSD species are homomorphic and emerged from autosomes relatively recently. To examine these issues, we plan to employ more sensitive cytogenetic methods to uncover “cryptic” sex chromosomes in GSD eyelid geckos.

10-15 Poster

SEX CHROMOSOME DIMORPHISM, OFFSPRING SEX ADJUSTMENT AND LIFE HISTORY IN BIRDS

Joanna Rutkowska [1, 2]

[1] *University of Arizona, Department of Ecology and Evolutionary Biology, 1041 E. Lowell, 85721, Tucson, USA*
[2] *Jagiellonian University, Institute of Environmental Sciences, Gronostajowa 7, 30-387, Kraków, Poland*

rutko@eko.uj.edu.pl

Despite increasing insight into the forces shaping evolution of sex chromosomes, the consequences of their dimorphism are poorly understood. Birds are especially suited to study such question because they exhibit striking dimorphism of Z and W sex chromosomes which is expressed in chromosome size and position of the centromere, and these traits vary among species, sometimes even between closely related ones. Because differences in chromosome morphology may affect the outcome of meiosis and because female birds are heterogametic, dimorphism in avian sex chromosomes could facilitate offspring sex adjustment in this taxon. Here I study whether species that may gain greater fitness benefits from the ability to adjust offspring sex, for example because of low breeding opportunities, exhibit higher sex chromosome dimorphism. I predict a negative relationship between sex chromosome dimorphism and clutch size. Chromosome asymmetry should also differ between atricial and precocial species and in relation to their sexual size dimorphism. To study whether higher dimorphism in sex chromosome size and shape covaries with life-history traits in birds, I used published karyotypes of over 150 bird species and information on their breeding biology. I will present results of analyses controlling for phylogenetic contrasts and discuss proximate and ultimate consequences of avian sex chromosome dimorphism.

10-16 Poster

SEX CHROMOSOMES, SPECIES RECOGNITION, AND EVOLUTION OF REPRODUCTIVE ISOLATION IN FLYCATCHERS

Stein A. Sæther [1], Glenn P. Sætre [2], Thomas Borge [2], Anna Qvarnström [3]

[1] *Netherlands Institute of Ecolgy, Department of Animal Population Biology, PO Box 40, 6666 ZG, Heteren, Netherlands*
[2] *University of Oslo, CEES, Department of Biology, PO Box 1050, Blindern, 0316, Oslo, Norway*
[3] *Uppsala University, Department of Animal Ecology, EBC, PO Box 40, 6666 ZG, Uppsala, Sweden*

s.saether@nioo.knaw.nl

Hybridization can help complete speciation when natural selection against it reinforces assortative mating between incipient species. However, hybridization also sets the stage for recombination to break genetic associations between traits used for species recognition and the mating preferences for them, rendering reinforcement unlikely. Here we show that reduced recombination rates due to physical linkage may have solved this problem in two hybridizing *Ficedula* flycatchers displaying evidence for reinforcement. Through analyses of the mating patterns of hybrids and cross-fostered offspring, we demonstrate that species recognition by females is inherited on the Z sex chromosome. Because the Z also hosts genes associated with low hybrid fitness and species-specific male plumage traits, our findings suggest that the sex chromosomes may be a hotspot for adaptive speciation.

10-17 Poster

NONRANDOM GENE CONTENT OF THE Z CHROMOSOME IN CHICKEN

Radka Storchova [1], Petr Divina [2]

[1] *Charles University in Prague, Department of Zoology, Vinicna 7, 128 44, Prague 2, Czech Republic*
[2] *Institute of Molecular Genetics AS CR, Department of Mouse Molecular Genetics, Videnska 1083, 142 20, Prague 4, Czech Republic*

radkas@natur.cuni.cz

Homogametic sex chromosomes (X and Z) play a prominent role in several fundamental evolutionary processes, such as speciation and sexual selection. This is the reason why considerable effort has been devoted to characterize the gene content of these chromosomes and determine the selective forces acting on sex-linked genes. Most studies of the X chromosomes in various animal species revealed an unusual complement of genes that are expressed preferentially or exclusively in one sex. However, the mechanisms underlying this phenomenon remain largely unresolved. In this work, we analyzed the gene content of the Z chromosome in chicken. Our analysis of the publicly available expressed sequence tags (EST) data revealed a significant underrepresentation of ovary-specific genes on the chicken Z chromosome. For the brain-expressed genes, we found a significant enrichment of male-biased genes but an indication of underrepresentation of female-biased genes on the Z chromosome. This report provides the first evidence for the nonrandom gene content of the homogametic sex chromosome in a species with heterogametic females. The comparison of the sex chromosome gene contents in heterogametic male and female systems will make it possible to decouple the effects of sex and heterogamety and thus, it may provide new and more general insight into the mechanisms responsible for the nonrandom complement of genes on the homogametic sex chromosomes.

10-18 Poster

MOLECULAR EVOLUTION OF A SEX-LINKED MARKER IN PALEARCTIC TREE FROGS OF THE HYLA ARBOREA GROUP

Matthias Stöck [1], Hélène Niculita [1], Sylvain Dubey [1], Nicolas Perrin [1]

[1] *University of Lausanne, Ecology and Evolution, Quartier Sorge, Biophore, CH-1015, Lausanne, Switzerland*

matthias.stoeck@unil.ch

European treefrogs (Hyla arborea) are male heterogametic, as recently revealed from a sex-specific marker fixed for different alleles (Berset-Brändli et al. 2006, Mol. Biol. Evol. 23, 1104–1106). We amplified, cloned and sequenced ~1kb of nuclear DNA incorporating this marker (5-22/p984), and studied its sex-specificity and sequence evolution within a molecular phylogenetic framework based on ~2.8 kb of mitochondrial and ~1kb of nuclear DNA that includes most Western Palearctic, several Eastern Palearctic and some Nearctic Hyla species. The marker 5-22/p984 represents a functional component of the Mediator transcription coactivator complex, widely conserved in metazoans. In Hyla, its coding region evolved mainly by insertions and deletions of base triplets (i.e. entire amino acids), but appears otherwise conserved. Some small intronic regions show a considerable sequence turnover. Sex-specificity was found within all European species from the H.arborea group (including several cryptic Circum-Mediterranean taxa), but not in H. meridionalis (the closest outgroup), supporting the hypothesis of an evolutionarily young Y chromosome (Berset-Brändli et al. 2007, J. Evol. Biol. 20, 1182-1188). However, phylogenetic patterns suggest that male and female 5-22/p984 alleles have started to diverge significantly after the emergence of the common Y chromosome, and independently so in the different taxa.

10-19 Poster

FUNCTIONS OF THE Y CHROMOSOME IN SILENE LATIFOLIA

Jitka Zluvova [1], Bohuslav Janousek [1], Jiri Zak [1], Adeline Berger [2], Elleni Michu [1], Francoise Moneger [2], Deborah Charlesworth [3], Ioan Negrutiu [2], Boris Vyskot [1]

[1] *Institute of Biophysics AS CR, v. v. i., Department of Plant Developmental Genetics, Kralovopolska 135, 612 65, Brno, Czech Republic*
[2] *Université de Lyon, ENS Lyon, Laboratoire RDP, IFR128 BioSciences Lyon-Gerland, 43 Allee d'Italie, 69364, Lyon, France*
[3] *University of Edinburgh, Institute of Evolutionary Biology, King's Buildings, West Mains Road, EH9 3JT, Edinburgh, United Kingdom*

jitka@ibp.cz

Theories of the sex chromosome evolution predict that the primary sex determination loci arose in a small "proto-Y" region, followed by accumulation of sexually antagonistic mutations with male-benefits in Y chromosome regions tightly linked with the sex-determining genes, creating further selection for suppressed recombination with the X-chromosome homologous regions. The subsequent separation of sexual organs in two separate individuals led step by step to the diversification of the male and female gene expression patterns resulting in sexual dimorphism. A well established model to study these early processes of sex chromosome evolution is a dioecious plant *Silene latifolia*. Based on the analyses of the Y chromosome deletion mutants, we have shown that the *S. latifolia* Y chromosome contains several genes indispensable for male reproduction. Some of them diverged to such extent that their absence is not complemented by their orthologues from a related hermaphroditic species [1]. Apart from the genes indispensable for male reproduction, the Y chromosome also contains "master regions" of genes involved in the sexual dimorphism [2].

[1] Zluvova et al. (2005) Evol. Dev. 7: 327-336. [2] Zluvova et al. (2006) PNAS 106: 18854-18859.

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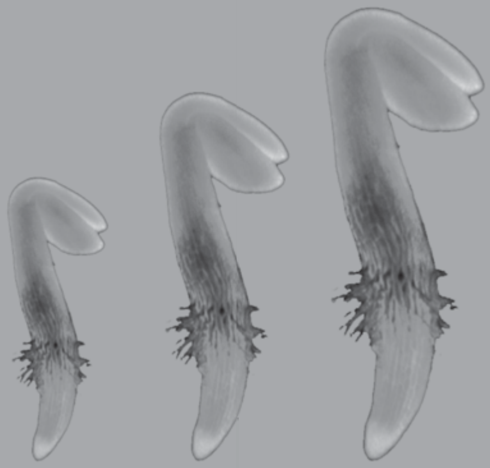
Gender perspective in evolutionary biology

11



Saturday August 25 *Location*: University building IX

Symposium 11: Gender perspective in evolutionary biology

ORGANIZERS: Malin Ah-King, Stockholm University, Sweden
Måns Andersson, Uppsala University, Sweden

14.00-14.30 **Marlene Zuk** (invited)
Role models and model systems: how gender bias affects our science

14.30-15.00 **Patricia Adair Gowaty** (invited)
Chance, time and the origins of adaptive, sex-neutral "sex roles"

15.00-15.20 **Margareta Segerståhl**
Novel systems view on eukaryotic sexual reproduction

15.20-15.50 *Coffee*

15.50-16.10 **Daniel Rankin**
Male harassment and the tragedy of the commons

16.10-16.30 **Krzysztof Hoffmann**
Can metaphors have a good sex?

16.30-16.50 **Hans Van Gossum**
Polychromatism in female damselflies (Insecta: Zygoptera): to be or not to be male-like?

16.50-17.10 **Shinichi Nakagawa**
The cheating and the cheated: a relatively complete picture of ‘hidden’ sexual selection

11-01 Talk

ROLE MODELS AND MODEL SYSTEMS: HOW GENDER BIAS AFFECTS OUR SCIENCE

Marlene Zuk [1]

[1] *University of California, Department of Biology, Riverside CA 92521, USA*

marlene.zuk@ucr.edu

All of us harbor ideas about sex and gender that color how we view the world. In addition to affecting our personal lives, these ideas also influence how we do science. Often unconsciously, pre-existing or underlying biases about male and female norms mean that we generate hypotheses and evaluate data about topics such as life history theory, sexual conflict, or reproductive behavior and morphology differently than we would if these biases did not exist. In addition, because of the tendency to see males as the norm and females as a variation or special case, females can be less studied than males, or their attributes can be missed. In effect, males become the model system, which poses difficulties in understanding the evolution of many traits.

11-02 Talk

CHANCE, TIME AND THE ORIGINS OF ADAPTIVE, SEX-NEUTRAL "SEX ROLES"

Patricia Adair Gowaty [1]

[1] *University of Georgia, Institute of Ecology, 30602, Athens, Georgia, USA*

gowaty@uga.edu

I will discuss the hypothesis that variance in number of mates due to demographic stochasticity sets the ecological stage so that selection favors adaptive flexibility in choosy and indiscriminate behavior of individuals, regardless of their sex and gender. This perspective on the origins of individually flexible behavior suggests that non-adaptive and adaptive fitness variances occur because of mechanisms affecting the interaction of only five variables: population size, the distribution of fitnesses of the breeding population, individual encounter rates with potentially mating opposite sex individuals, remating latencies, and individual survival probabilities. The hypothesis predicts among other things that (1) population relative fitness is higher when both females and males assess likely fitness outcomes of mating with alternative potential mates, before (2) responding flexibly, mating sometimes as indiscriminate and sometimes as choosy; (3) the number of potential mates that an individual will accept or reject; and (4) the frequency of sexual conflict over mating. Some of the predictions are alternative to those of classical sexual selection and parental investment theory, and thus this hypothesis may be able to explain more of the variation in gendered expression of sex-typical behavior observed in nature than classical sexual selection.

11-03 Talk

NOVEL SYSTEMS VIEW ON EUKARYOTIC SEXUAL REPRODUCTION

Margareta Segerståhl [1], Jörkki J. Hyvönen [1], Michael Patra [2]

[1] *Helsinki University of Technology, Laboratory of Computational Engineering, P.O.Box 9203, FIN-02015 TKK, Espoo, Finland*
[2] *Lund University, Physical Chemistry 1, Centre for Chemistry and Chemical Engineering, P.O.Box 124, SE-22100 Lund, Sweden*

mes@lce.hut.fi

In the study of sexual reproduction, the viewpoint of genetic inheritance predominates and central attention has been given to the way in which meiosis mixes parental genomes. Other aspects, such as alternation of generations, self-fertilization, and gamete dimorphism are known as epiphenomena of sex. Here, we argue that sexual dimorphism, the origin of which is generally attributed to the emergence of gamete dimorphism, should receive more general attention.

Differentiation of large and sessile versus small and motile gametes is generally seen as the key aspect of germ cell dimorphism and the sperm-egg phenomenon. We have, however, theoretically examined developmental mechanisms of gametogenesis and found that studies of germ cell size and motility are unlikely to provide explanatory answers when it comes to the overall complexity of sex determination biology. Therefore, we focused on identifying an evolutionary context in which eukaryotic sexual reproduction may have originated.

As is commonly known, many organisms combine sexual gametogenesis with formation of dormant resistant survival spores. We chose this to be the starting point and formulated a transition model where unicellular organisms alternate between active life and metabolically inactive dormancy. Critical point in the model is the entry into dormancy because this transition involves a trade-off between reproduction efficiency and survival probability.

Here, we show that the different ways of forming sexual gametes can be interpreted as alternative developmental solutions to the challenges presented by this model system. We also propose a novel role for genetic mixing in this transition context. Our findings strongly suggest that a general systems approach can combine the genetic viewpoint with developmental aspects of sexual reproduction, thereby delivering a novel holistic view on eukaryotic sexual reproduction.

11-04 Talk

MALE HARASSMENT AND THE TRAGEDY OF THE COMMONS

Daniel J. Rankin [1, 2], Hanna Kokko [2]

[1] *University of Bern, Institute of Zoology, Wohlenstrasse 50A, 3032, Hinterkappelen, Switzerland*
[2] *University of Helsinki, Laboratory of Ecological and Evolutionary Dynamics, Department of Biological and Environmental Sciences, PO Box 65 (Viikinkaari 1), 00014, Helsinki, Finland*

daniel.rankin@esh.unibe.ch

Sexual selection affects the fitness of the individuals involved. Any process which affects the fecundity and survival at the individual level should have an influence on population processes, particularly on population stability and extinction risk. However, empirical studies investigating the population-level consequences of sexual selection yield conflicting results, and the question remains relatively unexplored. Sexual conflict, where males and females negatively affect one another's fitness, is an area of sexual selection which should have profound consequences for populations. Here we present a model of sexual conflict in which males inflict a direct cost on female fitness. We show that costs inflicted by males can have dramatic consequences at the population-level. As the total harassment that a female incurs will be influenced by male density, increased mortality of females will shift the population to more biased male populations, increasing the level of harassment and ultimately resulting in extinction. To males, females can be seen as a resource over which they are competing. Hence, the population consequences of male sexual harassment can be seen as a tragedy of the commons. This raises the question of how a tragedy of the commons caused by sexual conflict will be avoided. A simple extension to the model reveals that extinction may be prevented when the benefit a male gains from harassing a female is dependent on population density. Such feedbacks between density and the mating system may explain why studies on the population consequences of sexual selection are often in disagreement. Sexual selection will therefore depend on, and have an influence on, the population ecology of the organisms involved. Male behaviour may not have such tragic consequences for populations as they would in the absence of ecological feedbacks.

11-05 Talk

CAN METAPHORS HAVE A GOOD SEX?

Krzysztof Hoffmann [1]

[1] *Adam Mickiewicz University, Faculty of Polish and Classical Philology, ul. Fredry 10, 61-701 Poznan, Poland*

krzysztof.hoffmann@gmail.com

One may claim that science (contrary to humanities) is immune to gender abuses for it founds its rationale behind so called 'objective reality' which structure is unalterable. Although confronting such view is tilting at windmills because of numerous tacit presumptions needed to be able to posit it, there is always an insignificant (from the point of view of whole research process) moment susceptible to all kinds of distortions and activation of biases. My aim is to trace back the process of translation of empirical data of evolutionary biology into result interpretations or hypothesis conceptualizations in order to reveal covert premises and strategies of the gender categorization. No language representation is free from (in fact metaphysically grounded) methods of hierarchization and organization – as such it produces forces of exclusion and power to subordinate (including e.g. embedding in anthropomorphic concepts or binary oppositions: male/female, primary/secondary, active/passive, relevant/irrelevant, etc.). According to Lakoff and Johnson metaphors we use are not only linguistic constructions but they are primarily cognitive constructs, which determine the way we think and act. Thus, the quest for abuses biologists commit in their texts may be considered not only as a struggle for futile linguistic political correctness but first and foremost as an effort to understand the insidious nature of set phrases and conceptual clichés which use is unaware for so many researchers.

11-06 Talk

POLYCHROMATISM IN FEMALE DAMSELFLIES (INSECTA: ZYGOPTERA): TO BE OR NOT TO BE MALE-LIKE?

Hans Van Gossum [1], Katleen Huyghe [2], Nathan Morehouse [3]

[1] *University of Antwerp, Evolutionary Biology Group, Groenenborgerlaan 171, B-2020, Antwerp, Belgium*
[2] *University of Antwerp, Laboratory for Functional Morphology, Universiteitsplein 1, B-2610, Wilrijk, Belgium*
[3] *Arizona State University, School of Life Sciences, AZ 85287-4501, Tempe, USA*

hans.vangossum@ua.ac.be

Sex-limited colour polymorphism occurs in a variety of animal taxa, with restriction to the female sex commonly encountered in many species of damselflies. In these insects, one female morph often resembles the male coloration (termed andromorph), whereas the other morph(s) appear(s) quite different from males in colour (gynomorph). It has been suggested these so-called andromorph females engage in male-mimicry, obscuring their sexual identity, to reduce unwanted male sexual harassment. Gynomorphs, in contrast, have to face excessive male sexual attention and as a consequence may suffer decreased fitness. Interestingly, different species of damselfly vary in how closely andromorph females resemble male models. Species where resemblance between male and andromorph female coloration is poor (at least to human eyes) have raised questions about whether male-mimicry is actually occurring, or whether some other mechanism may be responsible for maintaining the colour polymorphism in these species. Here, we evaluate two damselfly species, one where andromorph females appear to be excellent male mimics (*Ischnura elegans*), and one where andromorph females approximate male colour patterns less faithfully (*Enallagma cyathigerum*). Using spectra of the colour patterns of male and female morphs paired with the visual sensitivities of these organisms and the spectral properties of their environment, we ask whether males are able to discriminate between males and andromorph females on the basis of their coloration. We also evaluate whether *E. cyathigerum* andromorph females can be considered "imperfect" male mimics or simply another gynomorph.

11-07 Talk

THE CHEATING AND THE CHEATED: A RELATIVELY COMPLETE PICTURE OF 'HIDDEN' SEXUAL SELECTION

Shinichi Nakagawa [1], Ben J. Hatchwell [1], Terry Burke [1]

[1] *University of Sheffield, Department of Animal & Plant Sciences, S10 2TN, Sheffield, UK*

s.nakagawa@sheffield.ac.uk

The 'hidden' sexual selection that operates via extra-pair paternity plays an important role in shaping species with pair bonds and sometimes can be more important than 'apparent' sexual selection in such systems. It is often not recognized that extra-pair mating involves a cost-and-benefit relationship or a conflict of interest (i.e. sexual conflict) among four parties: pair males, pair females, extra-pair males and extra-pair females. Most empirical and theoretical studies to date have concentrated on investigating the characteristics and relationships of the first three parties, while the fourth party, extra-pair females, has been neglected. Here, we present a study that investigated the characteristics and relationships of these four parties in an island population of house sparrows, *Passer domesticus* (a sexually dimorphic species with biparental care). Microsatellite genotyping at 15 polymorphic loci showed that *ca* 10–15% of offspring in the 3-year study period resulted from extra-pair paternity. We identified characteristics of each of the four parties, including age, body size and body condition, that determined the distribution of extra-pair offspring. These results reveal an intricate cost-and-benefit relationship among these four parties. The closed nature of our study population, which has negligible immigration and emigration and allows life-time monitoring of individuals, has, to our knowledge for the first time, made it possible to construct a relatively complete picture of 'hidden' sexual selection where both the cheating and the cheated have a role to play.

11-01 Poster

MATE CHOICE COPYING WHEN BOTH SEXES FACE HIGH COSTS

Joachim G. Frommen [1], Anna K. Rahn [1], Stefanie H. Schroth [1], Nadine Waltschyk [1], Theo C. M. Bakker [1]

[1] *University of Bonn, Institute for Evolutionary Biology and Ecology, An der Immenburg 1, D-53121, Bonn, Germany*

t.bakker@uni-bonn.de

Mate choice is linked to costs such as time and energy effort or a higher risk of predation. Furthermore, reproduction with a partner of lower than average quality will reduce an individual's fitness. Copying the mate choice of conspecifics is a tactic to reduce such costs. Most studies dealing with mate-choice copying focused on females, as they are usually expected to invest more into reproduction. However, in species where males provide brood care both sexes face high costs. Little is known about mate-choice copying in such mating systems. Male three-spined sticklebacks, *Gasterosteus aculeatus* L., build nests and care for the offspring alone, facing a high reproductive investment. Thus, one would expect that both males and females copy the mate choice of others. We gave male and female sticklebacks the opportunity to court either a partner that was visibly courted by another individual or a partner that was not visibly courted. The results suggest, to our knowledge for the first time, that both sexes copy mate choice in a system where they both have high reproductive costs.

11-02 Poster

HAS THE HUMAN FEMALE PERMANENT BREAST EVOLVED TO SIGNAL PAST REPRODUCTIVE SUCCESS?

Jan Böhme [1]

[1] *Södertörns högskola, Life Sciences, 141 89, Huddinge, Sweden*

jan.bohme@sh.se

The human female breast is unique among mammals in that it is permanent from sexual maturity onwards. There is reasonable consensus that this is caused by sexual selection. There is, however, no consensus as to what kind of sexual selection. No proposed model has won general acceptance, and all models have palpable weaknesses. All hypotheses for sexual selection for permanent breasts implicitly or explicitly presume that the upright, "perky" ideal breast of the Western culture is what was selected for, although this shape cannot be expected to occur after the first pregnancy. However, several cultures have had quite different breast ideals. In addition, agriculture provided new incentives to prefer virginal breasts, not present earlier. The consequent possibility to accumulate – and thus inherit – property would have turned stepchildren into a nuisance that should be avoided. In patrilineal societies, an obvious way to do this is to prefer virginal brides. Once virginal brides become desirable, virginal breasts will soon be, too. Most sex traits in women other than breasts are neotenous, and thus provide a youthful appearance. In contrast, the other great apes not only lack neoteny in females, but an older female is more sexually desirable. This makes evolutionary sense in these species, because the survival rate of a female's first-born is considerably lower than that of subsequent offspring. This would reasonably not have been different for human beings at speciation. If anything, our altricial infancy should have put a higher survival premium on offspring of experienced mothers. Thus, there would seem to be a need for a marker in humans for experienced motherhood despite youthful appearance. I propose that the permanent breast is this marker, and that the droopy breast of a semelparous woman is the biological sexual signal, not the short-lived virginal breast. The breast would thus serve as an honest signal, but one that signals good experience rather than good genes.

11-03 Poster

SEXUAL CONFLICT IN PENDULINE TITS: CONSISTENCY OF OFFSPRING DESERTION

Ákos Pogány [1], István Szentirmai [1], Jan Komdeur [2], Tamás Székely [3]

[1] *Eötvös University, Department of Ethology, Pázmány Péter S. 1/c, H-1117, Budapest, Hungary*
[2] *University of Groningen, Animal Ecology Group, Centre for Ecological and Evolutionary Studies, P.O. Box 14, 9750 AA, Haren, The Netherlands*
[3] *University of Bath, Department of Biology and Biochemistry, BA2 7AY, Bath, United Kingdom*

apogany@ludens.elte.hu

Evolutionary interests of males and females are often different over care provisioning, since each sex may increase its own reproductive success by shifting care provisioning to its mate. One of the most obvious manifestations of this sexual conflict over parental care is offspring desertion, whereby the deserting parent leaves the burden of full care to its mate while itself searching for a new mate. Offspring desertion is a wide-spread behaviour across taxa, and in some species its frequency varies across and within populations. Here we investigate the mechanisms by which such variation emerges in a natural population of Eurasian penduline tit *Remiz pendulinus*. This passerine has one of the most diverse mating systems among birds with sequential polygamy (up to 7 mates in a breeding season) and solely uniparental care by either parent. We test whether intra-population variation in parental care is a result of individually consistent (but between-individually different) behaviour, or individually variable (or random) behaviour. Using a three-year dataset we show that offspring desertion by females is consistent between nests, while offspring desertion by males depends strongly on seasonal changes, since males desert early in the season and care for their nests later. Our results suggest that males and females use different strategies in caring/deserting decisions, and intra-population variation in parental care builds up by different mechanisms in the sexes; female variation is mainly due to between-individual variation, while male variation is due to within-individual variation. These contrasting strategies suggest complex evolutionary trajectories in breeding behaviour of species with variable breeding system such as the penduline tit.

11-04 Poster

NO INTRALOCUS SEXUAL CONFLICT OVER OPTIMAL HORN SIZE IN BIGHORN SHEEP

Jocelyn Poissant [1], Alastair J. Wilson [2], Marco Festa-Bianchet [3], David W. Coltman [1]

[1] *University of Alberta, Department of Biological Sciences, University of Alberta, CW 405, Biological Sciences Centre, T6G 2E9, Edmonton, Canada*
[2] *University of Edinburgh, Institute of Evolutionary Biology, Room 415, Ashworth Lab, EH9 3JT, Edinburgh, UK*
[3] *Université de Sherbrooke, Département de biologie, J1K 2R1, Sherbrooke, Canada*

poissant@ualberta.ca

Intralocus sexual conflict can occur when male and female evolutionary interests diverge for a trait. While such conflicts may be ubiquitous, they have very rarely been studied in natural populations. In this study, we tested for the presence of intralocus sexual conflict over optimal horn size in the highly sexually dimorphic bighorn sheep (*Ovis canadensis*). Sexual dimorphism in this species is believed to result from strong sexual selection favoring larger males with massive horns through male-male combat. Since females have much smaller horns than males, sexually antagonistic selection may be acting on the genetic component of the trait. We estimated quantitative genetic parameters within and between the sexes for variation in adult horn volume (HV) independent of body weight in a wild pedigreed population that has been studied for more than 35 years using the 'animal model'. We also tested for selection by contrasting lifetime reproductive success to HV breeding values. We found that HV has a significant additive genetic component in both sexes and that male and female horns have the potential to evolve independently (genetic correlation < 1). Due to an absence of sexually antagonistic selection on HV breeding values, we conclude that there is no intralocus sexual conflict over optimal HV in the studied population.

11-05 Poster

FIERCE FEMALES: VARIATION IN INTRASEXUAL AGGRESSION AMONG TUATARA

Kristina M. Ramstad [1], Jennifer A. Moore [1], Jeanine M. Refsnider [1]

[1] *Allan Wilson Centre, Victoria University of Wellington, School of Biological Sciences, PO Box 600, 6140, Wellington, New Zealand*

kristina.ramstad@vuw.ac.nz

Studies of intrasexual aggression have typically focused on males because their behaviour and morphology are dramatic and easily observed. Here we report on the first study of intrasexual aggression among female tuatara (*Sphenodon punctatus*). Tuatara are the last living representatives of the reptilian order Sphenodontia; they are endemic to New Zealand, sexually dimorphic, and highly territorial. We measured the proclivity for and type of intrasexual aggression among female and male tuatara during the 2007 mating season on Stephens Island. Individual tuatara were presented with a non-moving model tuatara, and their responses observed for at least thirty minutes. Aggressive responses to the model were recorded in 14 of 43 trials overall. Male and female tuatara were equally likely to respond aggressively to the model, but differed in their type of response. Male tuatara tended to engage in visual displays designed to avoid physical contact, such as head raises (88% of trials) and body inflation (38%). In no trial did a male tuatara attack the model. Female tuatara were less likely to engage in display tactics (head nods and body displays, 33% each) and more likely to attack the model than male tuatara. Females mouth-gaped at the model in 67% of trials and bit the model on the head in 33% of trials. Female tuatara may be faster to attack same sex intruders in their territory than males because the cost of fighting (risk of injury, lost energy, tail loss) is higher among male than female tuatara. Female tuatara are likely aggressive during mating season because they are defending territories and burrows in which they live. We expect that aggression among females would be even fiercer during the nesting season as females compete for nest sites.

Association mapping in evolutionary biology: emerging concepts and insights from model species

12

Saturday August 25 *Location*: Ekonomikum 1

Symposium 12: Association mapping in evolutionary biology: emerging concepts and insights from model species

ORGANIZERS:	Martin Lascoux, Uppsala University, Sweden Thomas Bataillon, University of Århus, Denmark Outi Savolainen, University of Oulu, Finland

14.00-14.30	**Carsten Wiuf** (invited) The coalescent as a tool for association mapping
14.30-15.00	**Isabelle Goldringer** (invited) Low linkage disequilibrium around strongly selected genes in experimental selfing populations
15.00-15.20	**Stephen Wright** Natural selection mapping in plant genomes
15.20-15.50	*Coffee*
15.50-16.10	**Peter Andolfatto** Hitchhiking effects associated with weakly beneficial amino acid substitutions in the Drosophila melanogaster genome
16.10-16.30	**Fabrice Roux** Genome-Wide Association mapping in Arabidopsis thaliana to identify genes causing quantitative resistance to the pathogen Pseudomonas viridiflava
16.30-16.50	**Koen Verhoeven** Epistasis, obstacle or advantage for association mapping?
16.50-17.10	**Jakob Mueller** Zooming in on genetic fine-scale mapping

12-01 Talk

THE COALESCENT AS A TOOL FOR ASSOCIATION MAPPING

Carsten Wiuf [1]

[1] *University of Aarhus, Bioinformatics Research Center, Aarhus, Denmark*

wiuf@birc.au.dk

This talk will take as starting point the coalescent process, which is a model that describes the genealogical relationship of genes in a population. After introducing the coalescent, various aspects of the coalescent will be covered in particular in relation to 1) how the coalescent can be used to gain insight into the structure of linkage disequilibrium, regions inherited identically by descent, and other biological quantities of relevance for association mapping; and 2) how the coalescent can be used explicitly in association mapping methods.

12-02 Talk

LOW LINKAGE DISEQUILIBRIUM AROUND STRONGLY SELECTED GENES IN EXPERIMENTAL SELFING POPULATIONS

Isabelle Goldringer [1], Anne-Laure Raquin [2], Bénédicte Rhoné [1], Nathalie Galic [1], Isabelle Bonnin [1]

[1] *INRA, UMR de Génétique Végétale, Ferme du Moulon, 91190, Gif sur Yvette, France*
[2] *Univ. Paris VII, LEGS, 91190, Gif sur Yvette, France*

isa@moulon.inra.fr

Dynamic management of genetic resources aims at maintaining the evolutionary processes in subdivided populations grown in contrasted environments. We considered whether studying the evolution of traits under natural selection together with molecular markers and candidate genes in wheat experimental populations can allow to identify the genetic bases underlying adaptive responses. After 10 generations, a significant differentiation was found for plant height, due to competition for light, and for flowering time due to adaptation to local climatic conditions. Selection within a given population locally reduces genetic variability at the selected genes and at neighbouring loci. This so-called hitch-hiking effect might be used to detect chromosomal regions under selection. In an experimental population, we documented the evolution over 17 generations of gene diversity and linkage disequilibrium (LD) in a 6cM region around a major plant height gene (*Rht-B1*). *Rht-B1* was under strong selection (s=0.15) and its variation in frequency accounted for 12% of the total trait evolution. Although the genetic effective population size was smaller at *Rht-B1* (N_{eg}=18) compared to the whole genome (N_{eg}=167), the decrease in gene diversity at the closest loci was similar to the one occuring on the rest of the genome. When computing the expected frequencies at linked markers due to *Rht-B1* selection, we found that the two most tightly linked loci were affected in the same (limited) range as observed. Such limited effect was imputed to the relatively high initial frequency (p=0.66) of the favourable allele (soft-sweep). We found a significant reduction in genetic diversity around a gene under selection, only for a resistance gene located within an exogenous introgression responsible for restrictions to recombination. This situation is favourable to candidate gene approaches where small LD around selected genes are expected rather than hitch-hiking mapping.

12-03 Talk

NATURAL SELECTION MAPPING IN PLANT GENOMES

Stephen I. Wright [1]

[1] *York University, Biology, 4700 Keele St, M3J1P3, Toronto, Canada*

stephenw@yorku.ca

Several distinct approaches have been used to study the genetic basis of adaptive evolution, including QTL mapping, association mapping and studies of DNA sequence polymorphism. Here, I discuss the application of the latter approach to the genomes of maize and Arabidopsis lyrata, and the potential and power of integrating this approach with the others, to go beyond the identification of candidate genes. In both maize and Arabidopsis lyrata, we see clear signatures of population bottlenecks, which alone can reduce diversity and increase

the variance among loci beyond the standard neutral model. We have used coalescent simulations in both of these systems to first fit simple models of demographic history, and second identify genes that show patterns which are inconsistent with the demographic model. The most extreme outliers from the best fit demographic model represent candidate regions for selection, and in both systems the combination of these approaches with QTL and association mapping should help overcome the limitations and false positives generated by individual approaches.

12-04 Talk

HITCHHIKING EFFECTS ASSOCIATED WITH WEAKLY BENEFICIAL AMINO ACID SUBSTITUTIONS IN THE DROSOPHILA MELANOGASTER GENOME

Peter Andolfatto [1]

[1] *University of California, San Diego, Biological Sciences, 9500 Gilman Drive MC0116, 92093, La Jolla, CA, U.S.A.*

pandolfatto@ucsd.edu

Several recent studies have estimated that a substantial fraction of amino acid divergence between Drosophila species was fixed by positive selection, using statistical approaches based on the McDonald-Kreitman test. However, little is yet known about the fitness effects of beneficial amino acid mutations. If adaptive protein evolution is indeed common, the signature of associated selective sweeps should be detectable in genome variability data. Here I document a strong negative correlation between the level of synonymous site polymorphism and the rate of protein evolution in highly recombining regions of the X chromosome of D. melanogaster. This pattern is a unique signature of adaptive protein evolution and suggests that adaptation is an important determinant of patterns of neutral variation genome wide, including regions of high recombination. By combining a genetic hitchhiking model with the McDonald-Kreitman approach, I estimate both the rate and strength of beneficial amino acid substitutions. I estimate that 50% of divergent amino acids were driven to fixation by positive selection and that most beneficial amino acid mutations are of weak effect, with average selection coefficients on the order of 10^{-4}. My findings imply that most adaptive substitutions between species will be difficult to detect in genome scans of selection and that small population sizes may limit the adaptive potential of species.

12-05 Talk

GENOME-WIDE ASSOCIATION MAPPING IN ARABIDOPSIS THALIANA TO IDENTIFY GENES CAUSING QUANTITATIVE RESISTANCE TO THE PATHOGEN PSEUDOMONAS VIRIDIFLAVA

Fabrice Roux [1], Matt Horton [2], Joy Bergelson [2]

[1] *Université des Sciences et Technologies de Lille 1, Laboratoire de Génétique et Evolution des Populations Végétales, UMR CNRS 8016, Bâtiment SN2, 59655, Villeneuve d'Ascq, France*
[2] *University of Chicago, Department of Ecology and Evolution, 1101 E. 57th Street, 60637, Chicago, USA*

fabrice.roux@univ-lille1.fr

Because pathogen species are a threat for crops and natural plant populations, a main challenge is to identify the genetic basis for natural resistance variation in plant species. Genome-Wide Association (GWA) mapping has been shown to be successful in *Arabidopsis thaliana* for identifying pathogen resistance genes involved in the qualitative response (hypersensitive response, HR) to the strain *Pseudomonas syringae*: Pst DC3000 (Aranzana *et al.* 2005). We applied this method in *A. thaliana* to identify the genetic basis of quantitative resistance to *Pseudomonas viridiflava*, a worldwide pathogen species affecting plant yield. Combining phenotyping (quantitative resistance) and genotyping (5,000 genome-wide SNPs) of 96 natural worldwide *A. thaliana* accessions, and a mixed-model approach for reducing the false-positive rate while maintaining statistical power, we identified *A. thaliana* genomic regions involved in the quantitative resistance to *P. viridiflava*. A study of the genomic regions around the significant SNPs led us to class candidate genes in 3 categories: i) disease resistance genes (TIR genes), ii) genes described in the literature as being involved in the response to pathogens, and iii) genes with sequence homologies to resistance genes in other species. Because the genotyping of 250,000 genome-wide SNPs are expected in 2007 for 192 *A. thaliana* accessions (1 SNP every 500 bp), it is expected to have a more precise genomic location of genes involved in the quantitative resistance to *P. viridiflava*.

12-06 Talk

EPISTASIS, OBSTACLE OR ADVANTAGE FOR ASSOCIATION MAPPING ?

Koen Verhoeven [1], Lauren M. McIntyre [2]

[1] *Netherlands Institute of Ecology, Multitrophic Interactions, PO Box 40, 6666 ZG, Heteren, Netherlands*
[2] *University of Florida, Gainesville, USA*

k.verhoeven@nioo.knaw.nl

Genomewide association mapping efforts face multiple challenges, ranging from low levels of linkage disequilibrium (which requires genotyping at a very large number of markers) to the confounding effects of population structuring and the complexity of the genetic architecture of the trait under study. In this study we use computer simulations to explore the effects of gene interactions, or epistasis, on the power to detect genes in an association mapping context. Epistasis is a crucial component of the genetic architecture of many biologically relevant traits, and the impression exists that it complicates gene mapping efforts. Traditionally, in QTL studies one-dimensional genome scans are performed to detect locus main effects. However, multi-locus genome scans that search for locus main and interaction effects jointly can have higher power to detect underlying QTL when epistasis is present. This approach emphasizes detection of QTL rather than partitioning their effects into main effects and interaction effects. We show that power to detect two loci when fitting full models (main effects plus interactions) is often larger when these loci act epistatically than when they act additively. Additionally, power for single locus detection may be improved compared to the additive model. Our coalescent-based simulations illustrate several other aspects of association mapping approaches, including model selection strategies and marker dataset reduction based on the genealogical information that is contained in the sample.

12-07 Talk

ZOOMING IN ON GENETIC FINE-SCALE MAPPING

Jakob C. Mueller [1]

[1] *Max Planck Institute for Ornithology, Dept. Behavioural Ecology & Evolutionary Genetics, D-82305, Starnberg-Seewiesen, Germany*

mueller@orn.mpg.de

The emerging conceptual frameworks developed to genetically map complex traits in human populations can be directly applied to study the genetic architecture of natural phenotypic variation in any organism. From a genomics perspective measures of linkage disequilibrium structures, evolutionary conservation patterns and selection signatures are particularly interesting. We derived general methods from information theory to estimate the correlational structure between genotypes and phenotypes and to estimate the level of evolutionary conservation for genomic elements. These methods will be presented with successful examples from genetic fine-scale mapping studies of human complex traits. The results will be discussed in the context of the problems “Where to search for association signals?“, “Which genetic markers (tagSNPs, microsatellites) are useful?” and “How to delimit association signals?”.

12-01 Poster

USING HAPLOID DRONES FOR MAPPING STUDIES IN HONEYBEES (APIS MELLIFERA)

Dieter Behrens [1], Michel Solignac [2], Ingemar Fries [3], Robin F. A. Moritz [1]

[1] *Universität Halle-Wittenberg, Biologie, Hoher Weg 4, 06099, Halle, Germany*
[2] *CNRS Université Paris-Sud, Populations, génétique et évolution, Avenue de la terrasse, 91118, Gif-sur-Yvette, France*
[3] *Swedish University of Agricultural Sciences, Department of Entomology, Ulls väg 16, 75007, Uppsala, Sweden*

dieter.behrens@zoologie.uni-halle.de

In honeybees drones emerge from unfertilized eggs, carrying a single set of chromosomes from their mother. Male haploidy greatly facilitates genome mapping of phenotypic traits in honeybees (*Apis mellifera*), because haploidy rules out any interaction between different alleles, which may interfere with distinct phenotype segregation.

A queen that is heterozygous at a specific marker will produce drone offspring with both alternative alleles represented at equal frequencies. The identification of markers linked to a specific trait will therefore be much simpler than in a diploid organism. The availability of several thousand polymorphic microsatellite markers from the honeybee genome sequence, and the high recombination rate of 19 cM/Mb in honeybees therefore allow for mapping approaches with an exceedingly high resolution.

In this study we tested drone larvae of a single queen for resistance against American Foulbrood (AFB), a severe honeybee brood disease. In a bulk segregant analysis, DNA-pools of susceptible and resistant drone larvae in an AFB infection bio-assay were tested for biased distributions of microsatellite alleles. After confirmation of promising loci by genotyping of individuals and subsequent fine mapping, we identified a candidate region with a putative major gene that is causing susceptibility to AFB infection in our experiments.

12-02 Poster

VARIATION IN INSULIN SIGNALLING PATHWAY GENES IN DROSOPHILA

Sara Guirao [1], Montse Aguadé [1]

[1] *Universitat de Barcelona, Departament de Genètica, Diagonal 645, 08028, Barcelona, Spain*

sguirao@ub.edu

Adult body size is a species characteristic with important effects on its physiology, life history and ecology. In most animals, it is achieved by controlling growth during development. In Drosophila melanogaster, body size presents parallel latitudinal clines in different continents, suggestive of its adaptive character. Genes involved in establishing adult body size are therefore good candidates to reveal the footprint of positive selection. Their extensive molecular and genetic dissection in D. melanogaster has validated that the insulin signalling pathway is the major pathway influencing body size through its effect on cell size and cell number. Furthermore, there is a correspondence between QTLs (Quantitative Trait Loci) for body size and the localization of the insulin signalling pathway genes. Nucleotide variation in a subset of these genes was studied within and between species in order to uncover possible selective events at different time scales.

12-03 Poster

ASSORTATIVE MATING AND FRAGMENTATION WITHIN DOG BREEDS

Susanne Björnerfeldt [1], Frank Hailer [2], Maria Nord [1], Carles Vilà [1]

[1] *Uppsala University, Dept of Evolutionary Biology, Norbyvägen 18d, 75236, Uppsala, Sweden*
[2] *Smithsonian Institution, National Zoological Park, Genetics Lab, Connecticut Av., NW, 20008, Washington, DC, USA*

hailerf@si.edu

There are around 400 internationally recognized dog breeds in the world today, with a remarkable diversity in size, shape, colour and behaviour. Breeds are considered to be uniform groups with similar physical characteristics, shaped by selection rooted in human preferences. This has led to a large genetic difference between breeds and a large extent of linkage disequilibrium within breeds. These characteristics are important for association mapping of candidate genes for diseases and therefore make dogs ideal models for gene mapping of human disorders. However, genetic uniformity within breeds may not always be the case. We studied patterns of genetic diversity within 164 poodles and compared it to 133 dogs from eight other breeds. This revealed hidden population structure within poodles leading to differences as large as those observed among other well-recognized breeds. Analysis of the groups identified within poodles suggests that they are the result of assortative mating imposed by breed standards and breeder preferences. Pedigree information for the last three generations confirms that matings have not taken place at random or within traditionally identified size classes in poodles. Patterns of genetic diversity in other breeds suggest that disruptive selection may be a common feature in many dog breeds. The strong genetic structure within dog breeds can increase the power of association mapping studies, but also represents a serious problem if ignored.

12-04 Poster

CANDIDATE GENE ASSOCIATION ANALYSIS FOR MALE COURTSHIP SONG CARRIER FREQUENCY IN DROSOPHILA MONTANA

Malgorzata Lagisz [1], Shuo- Y. Wen [2], Kirsten Klappert [3], Dominique Mazzi [4], Anneli Hoikkala [5], Mike G. Ritchie [6], Roger K. Butlin [7]

[1] *Newcastle University, School of Biology and Psychology, Ridley Building, NE1 7RU, Newcastle upon Tyne, UK*
[2] *South China Agricultural University, Department of Entomology, Guangzhou, 510642, Guangzhou, 510642*
[3] *EAWAG, Department of Aquatic Ecology, P. R. China, Guangzhou, Duebendorf, Switzerland*
[4] *ETH Zurich, Institute of Plant Sciences / Applied Entomology, Ueberlandstrasse 133, CH-8600, Zurich, Switzerland*
[5] *University of Jyväskylä, Department of Biological and Enviromental Sciences, Schmelzbergstrasse 9 / LFO, CH - 8092, Jyväskylä, Finland*
[6] *University of St Andrews, School of Biology, P.O. Box 35, 40014, St Andrews, UK*
[7] *University of Sheffield, Department of Animal and Plant Sciences, Harold Mitchell Building, KY16 9TH, Sheffield, UK*

m.m.lagisz@ncl.ac.uk

We examined the association between gene-specific markers of ten candidate genes and the carrier frequency of male courtship song in *D. montana*. Two isofemale lines of this species originating from Colorado, USA, and Oulanka, Finland, and significantly differing in song intrapulse frequency were crossed to generate an F2 laboratory generation. Ten candidate genes were sequenced for the original strains and the observed single-nucleotide polymorphisms and deletions were used to design PCR and PCR-RFLP based assays. Two polymorphisms, in the candidate genes *fruitless* and *ebony* showed significant ($P < 0.005$) associations with the song carrier frequency in the population tested. However, both genes are located on the same chromosome (3R) and seem to be closely linked. Interactions between other candidate genes have some weak associations with the trait of interest. These results suggest that *fruitless* and *ebony* should be examined in more detail to determine whether they have direct effects on song carrier frequency or mark other significant loci in the same chromosomal region.

12-05 Poster

ASSOCIATION BETWEEN POLYMORPHISM IN THE COL1 GENE AND FLOWERING TIME IN BRASSICA NIGRA

Martin Lascoux [1]

[1] *Uppsala University, Evolutiionary Functional Genomics, Norbyvägen 18D, 75236, Uppsala, Sweden*

martin.lascoux@ebc.uu.se

In a previous study we showed in a limited set of populations that variation at an indel, *Ind2*, located within the *BniCOL1* gene of *Brassica nigra* was associated to flowering time. Plants that were homozygotes for the short allele flowered early whereas homozygotes for the long allele flowered late, the heterozygotes being intermediate. In the present studywe have genotyped individuals from 25 populations, representative of the current distribution of *B. nigra* at *Ind2* as well as at 4 adjacent polymorphisms and assessed the relationship of these markers with flowering time. The presence of a significant relationship between polymorphism at *Ind2* and flowering time in some European populations and the fixation of *Ind2* for the short allele in southern populations was confirmed. Genotypic disequilibrium around *Ind2* was extensive and consequently polymorphism at markers located in the intergenic space between *BniCOL1* and *BniCOa* were also associated to flowering time. All populations from India and Ethiopia flowered early, had limited polymorphism at all five loci and were fixed for the short allele at *Ind2*. Finally, there was some evidence of selection at some of the markers, albeit weak. In conclusion, the data confirm the involvement of this genomic area in the control of flowering time but, due to the extensive linkage disequilibrium in this genomic area, do not allow the exact identification of the causal polymorphism.

12-06 Poster

PHENOTYPIC EVOLUTION IN A RADIAL NETWORK GENETIC ARCHITECTURE

Arnaud LE ROUZIC [1], Paul B. SIEGEL [2], Örjan CARLBORG [1]

[1] *Uppsala University, Linaeus Centre for Bioinformatics, BMC Box 598, Husargatan 3, 75124, Uppsala, Sweden*
[2] *Virginia Polytechnic Institute and State University, Department of Animal and Poultry Sciences, VA 2406-0306, Blacksburg, USA*

arnaud.lerouzic@lcb.uu.se

The genetic architecture of a quantitative trait influences phenotypic response to natural or artificial selection. One of the main motives of genetic mapping studies is yet to identify the contribution of more complex genetic architectures to phenotypic expression and variability. Large networks of connected genes have been reported, but there is an almost complete lack of information on how polymorphisms in these networks contribute to phenotypic variation and change: so far, most of our understanding comes from theoretical, model-based studies, and it is still difficult to assess how realistic the conclusions from this work are, as they lack empirical support. In this contribution, I illustrate the relationship between an empirically detected polymorphic, epistatic radial genetic network architecture and phenotypic evolution. I use a model-free approach to study, through individual-based simulations, the dynamic properties of this gene network.The results provide new insights to how epistasis can modify the selection response, buffer and reveal effects of major loci leading to a progressive release of genetic variation. I also illustrate the difficulty of predicting genetic architecture from observed selection response, and discuss mechanisms that might lead to misleading conclusions on underlying genetic architectures from Quantitative Trait Locus (QTL) in selected populations.

12-07 Poster

EXPLORING THE MOLECULAR BASIS FOR ATHLETIC PERFORMANCE TRAITS IN NORTH SWEDISH TROTTERS

Gabriella Lindgren [1], Ingrid Jacobsson [2], Aneta Ringholm [2], Knut H. Roed [3], Sofia Mikko [1], Leif Andersson [2]

[1] *Swedish University of Agricultural Sciences, Dept of Animal Breeding and Genetics, Uppsala, Sweden*
[2] *Uppsala University, Dept of Medical Biochemistry and Microbiology, Uppsala, Sweden*
[3] *Norwegian School of Veterinary Science, Dept of Basic Sciences and Aquatic Medicine, Oslo, Norway*

gabriella.lindgren@imbim.uu.se

The origin of the North Swedish trotter provides a unique opportunity to identify genes influencing body constitution and racing performance. The North Swedish trotter originates from the North Swedish horse that is a draught horse used in farming and forestry. It is well known that there has been some crossbreeding between Standardbreds and North Swedish trotters before obligatory paternity testing was introduced in Sweden. We hypothesize that we will be able to detect a gene flow that has occurred between Standardbreds and North Swedish trotters due to this cross-breeding, and a subsequent strong selection for racing performance in the North Swedish trotters. A remarkable improvement in racing performance of the North Swedish trotter has occurred during the last fifty years. We are using a population genomics approach to identify chromosome regions under positive selection to achieve our goals. Chromosome regions under strong positive selection are likely to harbor genes affecting morphological and physiological traits important for physical performance traits in this system. Presently, we compare the genetic makeup of North Swedish trotters (20 individuals), North Swedish horses (10 individuals) and Standardbreds (10 individuals) by performing a high-density genome scan. To date, 167 microsatellite markers have been analyzed within the horse material. Estimation of overall Fst values between the three horse breeds support that crossbreeding has occurred between the Standardbred and the North Swedish Trotter. Detection of genes that regulate racing speed is of particular interest as this could give a model for further studies of the genetic basis for complex traits such as muscle capacity and oxygen uptake.

12-08 Poster

GENOME-WIDE MAPPING QTLS OF MANDIBLE SHAPE IN A HETEROGENEOUS STOCK OF MICE

Nicolas Navarro [1], Christian P. Klingenberg [1]

[1] *University of Manchester, Faculty of Life Sciences, Michael Smith Building, M13 9PT, Manchester, United Kingdom*

nicolas.navarro@manchester.ac.uk

The mouse mandible, a structure of great importance for feeding, consists of parts that have different functions in the process of biting and chewing. Precise characterization of its genetic architecture is therefore important for understanding its evolutionary potential. Quantitative trait locus (QTL) mapping provides such data by detecting genomic regions that affect a given phenotype and estimating their effects. Conventional genetic designs for QTL mapping suffer from weak resolution and power to achieve this goal. There are, however, newly available designs and genomic resources that overcome these difficulties and afford unprecedented statistical power and genetic resolution.

We attempt to map loci affecting mandible shape using 1,700 mice from a heterogeneous stock (HS), which were each genotyped for 12,000 single nucleotide polymorphisms. HS mice were derived from the 50th generation of an intercross of eight inbred laboratory strains. Founder probabilities are reconstructed using a dynamic programming implemented in Happy. Geometric morphometric methods are used to quantify and analyse mandible shape. We used multiple multivariate regression to map QTLs. We used a parametric bootstrap approach to simulate a null hypothesis of infinitesimal model based on REML estimates of components of variance-covariance.

We find 258 potential QTLs. On these candidates, we build multiple QTLs models by subsampling and forward selection. Aggregating these models yields fifty to seventy loci having an effect on mandible shape. Confidence intervals of them are in average 2.5 Mb. QTL effects were re-estimated for each model on the total sample and averaged. The effects of different alleles of a given QTL on shape differ not only in their magnitude, but are also qualitatively different from each other in that they change different shape features. The overall pattern of integration of QTL effects reflects the developmental set-up of the mandible.

12-09 Poster

A GENOME WIDE DEFICIENCY SCREEN TO ASSESS THE GENETIC BASIS OF WING SHAPE VARIATION IN DROSOPHILA MELANOGASTER.

James S. Patterson [1], Casper J. Breuker [2], Christian P. Klingenberg [1]

[1] *The University of Manchester, Faculty of Life Sciences, Oxford Road, M13 9PT, Manchester, UK*
[2] *University of Exeter, Centre for Ecology and Conservation, Cornwall Campus, TR10 9EZ, Penryn, UK*

james.patterson@manchester.ac.uk

The *Drosophila* wing is an excellent model system for which development is understood in sufficient detail that the functioning of the whole system can be addressed. We are using the Exelixis collection of *Drosophila melanogaster* stocks, each with a small deficiency for a different genomic region on an otherwise isogenic background. We use geometric morphometrics to compare the wing shapes of flies with one copy of a deficiency to wild-type controls, and we have extracted information from databases of genome annotation and gene ontology to identify and locate candidate genes. From mean shape differences we can infer the effects of these genetic perturbations on the developmental pathways involved in wing formation. Many of the deficiencies from different genomic regions are affecting wing shape, indicating that numerous genes affect the development of the wing and are potential targets for the evolution of wing shape. Furthermore, most effects are small, and the mean shapes of the deficiency lines are evenly dispersed through the shape space. It appears that flies hemizygous for small regions of the genome have wing shapes close to the wild-type, suggesting that haploinsufficiencies of large effect for the genes involved in the development of the wing are rare. We observed that magnitude of effect is related to deletion size, viz. number or genes deleted, and in particular deletions with high proportions of genes with roles in general cellular structure and metabolic processes and not candidate genes per se. A corollary is that large deletions of genes with general continuous expression result in deficiencies, causing perturbations throughout development that ultimately affect the phenotype.

12-10 Poster

SIBLING SPECIATION IN ARCTIC DIPLOID DRABA (BRASSICACEAE)

Inger Skrede [1], Liv Borgen [1], Christian Brochmann [1], Loren Rieseberg [2]

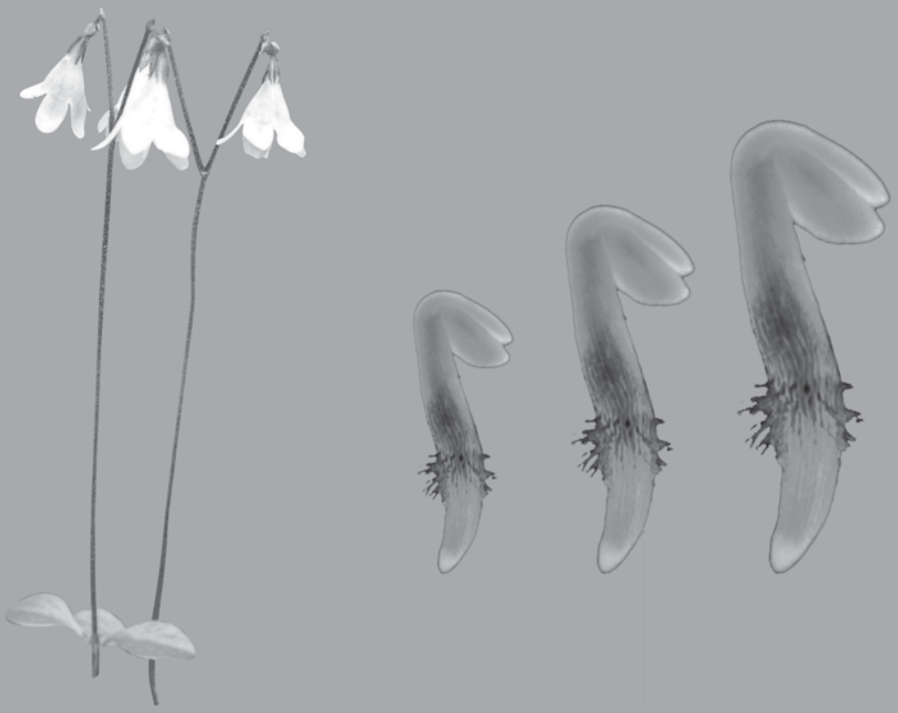
[1] *University of Oslo, Natural History Museum, P.O. Box 1172 Blindern, 0318, Oslo, Norway*
[2] *University of British Colombia, Department of Botany, 3529-6270 University Blvd, V6T 1Z4, Vancouver, Canada*

inger.skrede@nhm.uio.no

Incomplete to fully developed postzygotic sterility barriers within species were recently demonstrated in three circumpolar species of the genus *Draba*, suggesting numerous sibling species (Grundt *et al.*, 2006; PNAS, 103, 972-975). Because the three species are selfers and of recent, Pleistocene origin, Grundt *et al.* argued that hybrid sterility evolved quickly and possibly by genetic drift. The present study employs genetic mapping and quantitative trait locus (QTL) analyses to determine whether the sterility has a chromosomal or genic basis and, if the latter, whether the sterility is caused by interactions among alleles at a single locus or by interactions among alleles at different loci. A F2 population of 383 individuals was generated by crossing two *Draba nivalis* plants, one from Alaska and one from Norway (F1 hybrids were ~30 % fertile). All F2 plants have been tested for pollen viability, seed set, and growth rate, and were on average 62 % fertile for the two fertility measures. A microsatellite-enriched library has been made for *D. nivalis*, and 50 loci have been genotyped for all individuals. QTL analyses identified five loci underlying seed fertility and two affecting reduced pollen viability. Seed fertility QTLs were weakly underdominant, an observation most consistent with single locus sterility, such as that caused by chromosomal rearrangements. In contrast, pollen sterility QTLs exhibited additive inheritance patterns as might be expected for Dobzhansky-Muller incompatibilities. The small number of sterility QTLs is consistent with results from other plant groups, which imply that fewer loci contribute to hybrid sterility in plants than in *Drosophila*.

Evolutionary epidemiology and its implications for disease control

13



Tuesday August 21 *Location*: University building IX

Symposium 13: Evolutionary epidemiology and its implications for disease control

ORGANIZERS: Olivier Restif, University of Cambridge, UK
Sylvain Gandon, IRD, Montpellier, France

09.45-10.15	**Troy Day** (invited) The evolution of disease life histories
10.15-10.45	**Andrew Read** (invited) How to make an evolution-proof insecticide for malaria control
10.45-11.05	**Anne Deredec** Modelling strategies of genetic control of vector populations to fight against infectious diseases.
11.05-11.35	*Coffee*
11.35-11.55	**Florence Débarre** Evolutionary epidemiology of drug resistance in a spatial model
11.55-12.15	**Gabriel Perron** Source-sink dynamics shape the evolution of antibiotic resistance and its pleiotropic fitness cost
12.15-12.35	**Anna-Liisa Laine** Evolution of parasite transmission in a natural plant-pathogen metapopulation
12.35-14.00	*Lunch*
14.00-14.20	**Jacobus de Roode** Virulence evolution in monarch butterfly parasites
14.20-14.40	**Lucie Salvaudon** Host-parasite genotypic specificity: effects of host variation on parasite evolution.
14.40-15.00	**Isabel Gordo** Patterns of genetic variation in pathogen populations
15.00-15.20	**Daniel Wilson** Tracing the host species of human food-borne infections
15.20-16.00	*Coffee*

13-01 Talk

THE EVOLUTION OF DISEASE LIFE HISTORIES

Troy Day [1]

[1] *Queen's University, Biology and Mathematics, Jeffery Hall, K7L3N6, Kingston, Canada*

tday@mast.queensu.ca

I will present some theoretical results that link within-host dynamics of pathogen replication to between host epidemiological and evolutionary dynamics. One of the main novelties of the approach I will present lies in its ability to make short-term evolutionary predictions without requiring explicit knowledge of the within-host dynamics of pathogen replication. The core ingredients of the approach are genetic covariance functions for epidemiological parameters over the course of an infection. This framework allows one to predict how disease life histories (i.e., the temporal pattern of transmission and mortality during an infection) are expected to evolve. The approach will be illustrated with an example taken from research on malaria.

13-02 Talk

HOW TO MAKE AN EVOLUTION-PROOF INSECTICIDE FOR MALARIA CONTROL

Andrew Read [1], Penny A. Lynch [2], Matthew B. Thomas [3]

[1] *University of Edinburgh, Institutes of Evolutionary Biology & Immunology and Infection Research, West Mains Road, Edinburgh EH9 3JT, UK*
[2] *Open University, Department of Mathematics, Milton Keynes, UK*
[3] *CSIRO Entomology, Canberra, Australia*

a.read@ed.ac.uk

The history of malaria control is one of eventual failure in the face of pathogen and vector evolution. The timescales of this evolution are usually outwith commercial time horizons, but the costs of bringing new control tools to market can be enormous (in excess of $US100 million for chemical insecticides). We should develop tools which last, yet with very rare exceptions the default position has been to worry about evolution only after a control measure is beginning to fail. Work we have been doing with entomopathogenic fungi suggests that it should be possible to evolution-proof insecticides directed against malaria. This is because disease control need not require mosquito control. The critical issue is to maximise transmission reductions while minimising selection for resistance. This should be attainable with biopesticides and, with some imagination, with chemical insecticides too. Indeed, it should be possible to make a pesticide that controls malaria forever, even in the face of standing genetic variation for resistance in mosquito populations.

13-03 Talk

MODELLING STRATEGIES OF GENETIC CONTROL OF VECTOR POPULATIONS TO FIGHT AGAINST INFECTIOUS DISEASES.

Anne Deredec [1], Austin Burt [2], H. Charles J. Godfray [3]

[1] CPB,Imperial College London, Silwood Park campus, SL57PY, Ascot, United Kingdom
[2] Imperial College London, Silwood Park campus, SL5 7PY, Ascot, United Kingdom
[3] University of Oxford, Department of Zoology, South Parks Road, OX1 3PS, Oxford, United Kingdom

a.deredec@imperial.ac.uk

Despite the improvement in our ability to cure and prevent infectious diseases through the last century, some vector-borne infectious diseases such as malaria remain a plague in some parts of the world. Some strategies aiming at controlling the vector populations have been considered and applied, but they mainly relied on using insecticides. If some attempts have been successful, they also have given rise to resistance. New control methods are desperately needed. Better knowledge of vector genomes, discovery of genetic mechanisms and development of genetic engineering methods now enable us to consider seriously the idea of engineering vectors to reduce the spread of diseases. Among the different genetic drive mechanisms put forward, Homing Endonuclease Genes (HEGs) - some site-specific selfish genes that exploit the recombinational repair system of the cell to copy themselves into a defined DNA sequence and may be used to knock out existing genes or knock in new genes - appear particularly promising. To reduce disease transmission by vectors, one can aim at depleting their population or at inducing refractoriness in it. Population depletion can be achieved by imposing a genetic load to it, but also by biasing the sex-ratio towards male, and HEG-based constructs may be engineered for these purposes. In the context of a refractoriness strategy, this drive mechanism could also be used to replace the existing population by a population with reduced or annihilated ability to transmit the parasite. Prior to any practical application, it is necessary to study every strategy, and try to establish the most efficient, the safest and the most reliable one. Here, by using deterministic population genetics models, we aim to investigate the efficiency of these strategies.

13-04 Talk

EVOLUTIONARY EPIDEMIOLOGY OF DRUG RESISTANCE IN A SPATIAL MODEL

Florence Débarre [1], Thomas Lenormand [2], Sylvain Gandon [1]

[1] CNRS, GEMI, IRD, 911 avenue Agroplois, 34394, Montpellier, France
[2] CNRS, CEFE, 1919, route de Mende, 34293, Montpellier, France

florence.debarre@ens.fr

The spread of drug-resistance in infectious diseases is an ever increasing source of concern. To better understand the evolutionary dynamics of drug resistance we analysed a spatial model in which transmission occurs locally but where the hosts (infected or not) can move among sites. Only a fraction of the environment is treated. This model extends previous population genetics studies on clines to an epidemiological setting. We find that there is a critical size of the treated area below which migration from untreated populations prevents resistant strains from persisting. We show that this critical size depends on the amount of migration, the intensity of selection for drug resistance in the treated area, but also on the type of resistance costs. Our study has important implications for the management of drug-resistance, and provides a new framework at the interface between population genetics and epidemiology.

13-05 Talk

SOURCE-SINK DYNAMICS SHAPE THE EVOLUTION OF ANTIBIOTIC RESISTANCE AND ITS PLEIOTROPIC FITNESS COST

Gabriel G. Perron [1], Andrew Gonzalez [2], Angus Buckling [1]

[1] *Oxford University, Department of Zoology, South Parks Road, OX1 3PS, Oxford, UK*
[2] *McGill University, Department of Biology, 1205 Ave Dr.Penfield, H3A 1B1, Montreal, PQ, Canada*

gabriel.guimond-perron@zoo.ox.ac.uk

Understanding the conditions that favour the evolution and maintenance of antibiotic resistance is a central goal of epidemiology. A crucial feature explaining the adaptation to harsh, or 'sink', environments is the supply of beneficial mutations via migration from a 'source' population. Given that antibiotic resistance is frequently associated with antagonistic pleiotropic fitness costs, increased migration rate is predicted not only to increase the rate of resistance evolution but also to increase the probability of fixation of resistance mutations with minimal fitness costs. Here we report *in vitro* experiments using the nosocomial pathogenic bacteria *Pseudomonas aeruginosa* that support these predictions: increasing migration rate into environments containing antibiotics increased the rate of resistance evolution and decreased the associated costs of resistance. Consistent with previous theoretical work, we found that resistance evolution arose more rapidly in the presence of a single antibiotic than two, and when bacteria were exposed to two antibiotics sequentially (cycling therapy) compared with simultaneously (bi-therapy). Furthermore, pleiotropic fitness costs of resistance to two antibiotics were higher than for one antibiotic, and were also higher under bi-therapy than cycling therapy, although the cost of resistance depended on the order of the antibiotics through time. These results may be relevant to the clinical setting where dispersal is known to be important between chemotherapeutically treated patient and demonstrate the importance of ecological and evolutionary dynamics in the control of antibiotic resistance.

13-06 Talk

EVOLUTION OF PARASITE TRANSMISSION IN A NATURAL PLANT-PATHOGEN METAPOPULATION

Anna-Liisa Laine [1]

[1] *University of Helsinki, Department of Biological and Environmental Sciences, PO Box 65 (Viikinkaari 1), 00014, University of Helsinki, Finland*

anna-liisa.laine@helsinki.fi

Despite the threats imposed by disease to humans, crops and livestock, surprisingly little is understood of how polymorphism is maintained in pathogen populations and how their transmission potential evolves. Here, using the naturally occurring interaction between an obligate fungal pathogen, *Podosphaera plantaginis* and its perennial host, *Plantago lanceolata*, I demonstrate that pathogen evolution is strongly coupled with its epidemiological dynamics. Annual surveys of over 3000 host populations have demonstrated that *Po. plantaginis* persists as a metapopulation in its host populations through frequent extinction and colonization events. Despite the rapid turnover of local populations, reciprocal cross inoculation experiments have demonstrated that the pathogen has adapted locally to its host populations. In fact, the metapopulation setting is tightly linked with the evolutionary potential of *Po. plantaginis* - The scale of local adaptation extends beyond local host populations reflecting the dispersal ability of *Po. plantaginis*. Furthermore, evolution of transmission is coupled with adaptation to the heterogeneous environment of the interaction. Polymorphism may be maintained through life-history trade-offs mediated by variation in temperature. These trade-offs call into question parasite fitness estimates based on a single life-history stage. I discuss alternative methods for calculating pathogen fitness, and the challenges of accounting for spatial reality in experimental studies of pathogen evolution.

13-07 Talk

VIRULENCE EVOLUTION IN MONARCH BUTTERFLY PARASITES

Jacobus C. De Roode [1], Sonia Altizer [1]

[1] *University of Georgia, Institute of Ecology, GA 30602, Athens, USA*

jaapderoode@hotmail.com

Theory has shown that parasites could evolve virulence (i.e. parasite-induced host mortality) as a consequence of selection maximizing fitness: in order to transmit between hosts, parasites must exploit their hosts, simultaneously damaging host tissues and increasing the chances of killing their host. Thus, higher transmission rates should come at the cost of higher mortality rates. Although this 'trade-off' model has been studied extensively by theoreticians, empirical support is still critically lacking. We studied the protozoan parasite *Ophryocystis elektroscirrha* in its natural host, the monarch butterfly (*Danaus plexippus*). We infected monarchs with cloned parasite genotypes obtained from wild populations, and assessed parasite transmission potential and host longevity. We found that genotypes producing more transmission stages also caused higher virulence, thus supporting theoretical assumptions. However, the relationship between transmission potential and virulence importantly depended on the geographic origin of hosts and parasites. Our results imply that selection on transmission rates is a major factor driving virulence evolution, and can explain why parasites harm their hosts. Moreover, population-specific host-parasite interactions apparently dictate the exact shape of the virulence-transmission relationship, and with that the adaptive level of parasite virulence in a population.

13-08 Talk

HOST-PARASITE GENOTYPIC SPECIFICITY: EFFECTS OF HOST VARIATION ON PARASITE EVOLUTION.

Lucie Salvaudon [1], Virginie Héraudet [1], Jacqui A. Shykoff [1]

[1] *Université Paris-Sud, CNRS, Laboratoire Ecologie, Systématique et Evolution, Bat 360, 91400, Orsay, France*

lucie.salvaudon@u-psud.fr

Evolution of parasites is inextricably linked to their hosts. The successful establishment of a parasite within a host and the diversion of resources toward its own transmission involve a strong and direct interaction between pathogen and host. Hence, we might expect that many traits involved in the epidemiology of a given parasite strain, such as its transmission rate or virulence, will not only depend on its own genotype but also on the type of host encountered. Such genotype by genotype specificity as been widely investigated for qualitative traits (gene for gene and matching allele systems), but studies on quantitative aspects of host-parasite specificity are only at the beginning. This type of interaction might, however, play a crucial role in parasite (and host) adaptation and thus in the outcome of pathogen epidemics. We experimentally investigated genotype specific interactions in infections of *Hyaloperonospora arabidopsis* (= *parasitica*), a natural pathogen of the Brassicaceae *Arabidopsis thaliana*. Cross inoculations between several parasite strains and host lines revealed that parasite transmission and aggressivity were indeed under the shared control of both protagonists. This specificity of interaction could even be found at a small geographical scale, among parasite strains originating from the same population. Host-parasite specificity also resulted in a decoupling of the relationship between host and parasite fitness. High parasite fitness, measured as transmission success, was not necessarily associated with low host fitness, estimated as seed production. We propose that different levels of compatibility, dependent on genotype by genotype interactions, might lead to different amounts of resources being available for host and parasite reproduction and thus mask the expected negative relationship between host and parasite fitness. This hypothesis implies that parasite adaptation toward optimal virulence may be slowed when parasite fitness traits are host genotype specific and when hosts are diverse enough such that parasites have a high probability of encountering different host genotypes.

13-09 Talk

PATTERNS OF GENETIC VARIATION IN PATHOGEN POPULATIONS

Isabel Gordo [1], Paulo R. A. Campos [2]

[1] *Instituto Gulbenkian de Ciência, Oeiras, Portugal*
[2] *Universidade Federal Rural de Pernambuco, Physics Departament, Dois Irmaos, Recife-PE, Brasil*

igordo@igc.gulbenkian.pt

Genetic variation in pathogen populations may help us understand their epidemiology and evolution. Here we study a model for assessing the levels and patterns of genetic diversity in pathogen populations. The population is structured into many small subpopulations, which correspond to their hosts, that are connected according to a specific type of contact network: fully connected or scale free networks. Pathogens transmit between hosts, where they grow and mutate until elimination by the host immune system. We show how our model is closely related to the classical SIS model in epidemiology and find that: depending on the relation between the rate at which pathogens are eliminated by the immune system and the intrahost effective population size, pathogen genetic diversity increases with R0 or peaks at intermediate R0 levels; patterns of genetic diversity in this model are in general similar to those expected under the standard neutral model, but in a scale free network and for low values of R0 a distortion in the neutral mutation frequency spectrum can be observed; highly connected hosts show higher levels of genetic variation, lower levels of genetic differentiation and larger values of Tajima's D. Furthermore we observe that for low values of R0, very heterogeneous host contact structures lead to lower levels of pathogen diversity.

13-10 Talk

TRACING THE HOST SPECIES OF HUMAN FOOD-BORNE INFECTIONS

Daniel J. Wilson [1], Edith Gabriel [1], Howard Leatherbarrow [2], Peter Diggle [1], Andrew Fox [3], Paul Fearnhead [1]

[1] *Lancaster University, Maths and Statistics, LA1 1WA, Lancaster, United Kingdom*
[2] *Liverpool University, Liverpool Veterinary College, Liverpool, United Kingdom*
[3] *Health Protection Agency, Manchester Royal Infirmary, Manchester, United Kingdom*

d.j.wilson@lancaster.ac.uk

By exploiting the genetic heterogeneity and structure inherent to the gastro-enteric pathogen *Campylobacter jejuni*, we inferred the source of human infections. Using newly-developed genealogical-based methods that account for differences not only in gene frequencies, but also linkage disequilibrium between source populations, we estimated the relative proportion of human cases attributable to different animal hosts and the environment. In addition we applied a coalescent model to estimate the relative contribution of mutation and recombination to evolutionary change in the pathogen, and to date the split time with the sister species *C. coli*, based on calibrating the mutation rate with temporally-spaced gene sequences.

13-01 Poster

DYNAMICS AND SPECIFICITY OF ADAPTATION TO SUBLETHAL CONCENTRATIONS OF PESTICIDES IN PHYTOPHTHORA INFESTANS

Stefan Bosmans [1], Arjan G. M. De Visser [1], Alfons J. M. Debets [1], Rolf F. Hoekstra [1]

[1] *Wageningen UR, Genetics, Arboretumlaan 4, 6703 BD, Wageningen, Netherlands*

stefan.bosmans@wur.nl

Adaptation to sub-lethal concentrations of a pesticide can potentially culminate into resistance. Here, we test the likelihood of this risk using laboratory evolution experiments with the potato late blight pathogen *Phytophthora infestans*. We serially transferred zoospores from two sensitive isolates on medium with a sub-lethal concentration of metalaxyl or cyazofamid, and measured the growth rate of evolved lines on a range of pesticide concentrations. Growth rate increased in all cases, but more rapidly for metalaxyl than for cyazofamid. After 10 transfers, we isolated single zoospores that showed stable adaptation to the selective agent. The dynamics and specificity of adaptation to metalaxyl were consistent with earlier observations, as it occurred fast and resistance was also significant at higher concentrations. Adaptation to cyazofamid, however, was specific for the selection conditions as it did not increase growth at higher concentrations.

13-02 Poster

EXPERIMENTAL EVOLUTION OF PARASITE LIFE-HISTORY TRAITS IN STRONGYLOIDES RATTI (NEMATODA)

Steve Paterson [1], Rebecca Barber [1]

[1] *University of Liverpool, School of Biological Sciences, Crown Street, L69 7ZB, Liverpool, UK*

S.Paterson@liv.ac.uk

Evolutionary ecology predicts that parasite life-history traits, including a parasite's survivorship and fecundity within a host, will evolve in response to selection and that their evolution will be constrained by trade-offs between traits. Here we test these predictions using a nematode parasite of rats, Strongyloides ratti, as a model. We performed a selection experiment by passage of parasite progeny from either early in an infection ('Fast' lines) or late in an infection ('Slow' lines). We found that parasite fecundity responded to selection but that parasite survivorship did not. We found a trade-off mediated via con-specific density-dependent constraints; namely that Fast lines exhibit higher density-independent fecundity than Slow lines but that Fast lines suffered greater reduction in fecundity in the presence of density-dependent constraints than Slow lines. We also found that Slow lines both stimulate a higher level of IgG1, which is a marker for a Th2-type immune response, and show less of a reduction in fecundity in response to IgG1 levels than for Fast lines. Our results confirm the general prediction that parasite life-history traits can evolve in response to selection and indicate that such evolutionary responses may have significant implications for the epidemiology of infectious disease.

13-03 Poster

THE EVOLUTION OF THE TRIATOMINE BUGS

James S. Patterson [1, 2]

[1] The University of Manchester, Faculty of Life Sciences, Oxford Road, M13 9PT, Manchester, UK
[2] London School of Hygiene and Tropical Medicine, Keppel Street, WC1E 7HT, London, UK

jamessimonpatterson@yahoo.co.uk

Triatomine bugs (Hemiptera: Reduviidae: Triatominae) are the vectors of Chagas disease in South and Central America. Chagas disease predominantly affects poor rural communities with simply constructed housing susceptible to infestation by triatomines. Chagas disease is restricted to the Americas largely due to the limited distribution of triatomine bugs. The global diversity of triatomines is ~130 species, of which only ~10% are know to occur outside the Americas, one species (*Triatoma rubrofasciata*) is tropicopolitan, and the others are concentrated on the Indian subcontinent (*Linshcosteus spp.*) and adjacent south east Asian island groups (*Triatoma spp.*). The Objective of the studies presented was to elucidate the broader phylogeny of Triatominae (in particular between Old and New World lineages) and their relationships with other reduviid subfamilies. Combined head and wing morphometric and molecular genetic analyses of New World and Old World Triatominae have revealed patterns of convergent morphological evolution (among New World and Old World *Triatoma*) and striking examples of strongly divergent morphological evolution (between Old World *Triatoma* and the geneus *Linshcosteus*). Applying a molecular clock based on the rate of sequence divergence for a fragment of ribosomal DNA (D2-28S) calibrated to the fossil record and vicariant events in geological time it has been possible to reconstruct a likely evolutionary history for the Triatominae and the Reduviidae as a whole. The weight of evidence presented supports a polyphylectic origin for blood-feeding for the Triatominae. The apparent independent development of blood feeding among the main lineages of the Triatominae represented by the genera *Triatoma* and *Rhodnius* highlights a fundamental biological difference among important vector species. This difference is likely to become evident in the eventual post genomic era in studies of vector/parasite interactions and it highlights the importance of sequencing genomes from different vector genera.

13-04 Poster

MAINTENANCE OF POLYMORPHISM IN GENE-FOR-GENE INTERACTIONS: INFLUENCE OF EPIDEMIOLOGY AND ECOLOGICAL FACTORS

Aurelien Tellier [1], James K. M. Brown [1]

[1] John Innes centre, Disease and Stress Biology, Colney, NR47UH, Norwich, United Kingdom

aurelien.tellier@bbsrc.ac.uk

Understanding the mechanisms that promote long term polymorphism at loci involved in plant-parasite recognition (gene-for-gene relationships) is a fundamental problem in evolutionary ecology. Co-evolution implies the existence of indirect frequency-dependent selection between host and parasite alleles. Polymorphism can only be maintained in both organisms if there is also negative, direct frequency-dependent selection (FDS), such that the intensity of natural selection for host resistance or parasite virulence declines with increasing frequency of that trait itself (Tellier and Brown, *Proc. Roy. Soc. B,* 2007).

It is first shown that direct FDS does not occur in monocyclic diseases (one parasite generation per host generation) in which only biotic and abiotic environmental conditions determine the size of the primary inoculum, and thus the severity of epidemics. On the other hand, maintenance of polymorphism occurs at high auto-infection rates in polycyclic diseases where parasites undergo several generations per host generation. Perenniality, a plant life history trait, also meets the theoretical requirement by generating direct FDS on host resistance. The host population's response to parasite selection is affected by the memory of past selective events stored in the growing population with a low death rate in the absence of disease. It is argued that because plant epidemics are highly dependent on environmental conditions, epidemiological models assuming overlapping host generations and density-dependent disease transmission (SIR like models) describe only a subset of plants-parasite co-evolutionary systems. Moreover, if fitness costs determine whether genetic polymorphism in a coevolving host-parasite pair is possible, the ecology of the host and its parasite determines whether polymorphism is in fact maintained.

Host-parasite evolution: consequences of parasite communities and host species assemblages

14

Friday August 24 *Location*: Ekonomikum 4

Symposium 14: Host-parasite evolution: consequences of parasite communities and host species assemblages

ORGANIZERS: Mark Brown, University of Dublin Trinity College, Ireland
Thierry Rigaud, Université de Bourgogne, France

9.45-10.15 **Dieter Ebert** (invited)
Interactions between hosts and multiple parasites: studies of Daphnia and its microparasites

10.15-10.45 **Sylvain Gandon** (invited)
Epidemiology and evolution of multihost parasites

10.45-11.05 **David Hughes**
Cordyceps infection of ants in a tropical rainforest: much more than meets the eye

11.05-11.35 *Coffee*

11.35-11.55 **Mario Ruiz-González**
Evolution and dynamics of one parasite with multiple hosts: epidemiology and population genetics of a trypanosomatid of bumble bees

11.55-12.15 **Guislaine Refrégier**
Identifying multi-host species, a crucial step in detecting host shifts from co-phylogeny analyses: the case of the fungal Microbotryum violaceum species complex

12.15-12.35 **Amy Pedersen**
Phylogeny and geography predict pathogen host range in wild primates and humans

12.35-14.00 *Lunch*

14.00-14.20 **Mike Boots**
Modelling the evolutionary implications of conflict between parasites with different transmission modes

14.20-14.40 **Simon Fellous**
Interactions between parasite doses and the host food availability on the outcome of mosquito coinfection by two parasite species

14.40-15.00 **Sandra Lass**
Co-infection with micro- and macroparasites: evidence of indirect interactions and a role for timing?

15.00-15.20 **Emilie Vautrin**
Dynamics and evolution of multiple infections with vertically transmitted symbionts

15.20-16.00 *Coffee*

14-01 Talk

INTERACTIONS BETWEEN HOSTS AND MULTIPLE PARASITES: STUDIES OF DAPHNIA AND ITS MICROPARASITES

Dieter Ebert [1]

[1] *Universität Basel, Zoology, Evolutionary Biology, Vesalgasse 1, 4051, Basel, Switzerland*

dieter.ebert@unibas.ch

In natural populations hosts frequently harbor more than one parasite. This is expected to have drastic consequences for the ecology (e.g. host - parasite interactions, parasite - parasite interactions, community composition) and evolution (virulence, resistance, competition) of the antagonists. In a series of investigations we addressed the general and specific consequences of multiple infections. In longitudinal field studies in populations of Daphnia we found that the frequency of multiple infections can be substantial. The same studies suggested that multiple parasites increase the negative effects on the host. In experiments we found that host population density and host extinction risk increases with increasing number of parasites in the mesocosms. However, parasite persistence strongly dependent on the specific competitors. Examples will be used to illustrate the general effects of being multiple infected and contrast this with aspects of specific interactions.

14-02 Talk

EPIDEMIOLOGY AND EVOLUTION OF MULTIHOST PARASITES

Sylvain Gandon [1]

[1] *CNRS, Génétique et Evolution des Maladies Infectieuses, IRD, 911 avenue agropolis, 34394, Montpellier, France*

sylvain.gandon@mpl.ird.fr

Multihost parasites can infect different types of hosts or even different host species. Epidemiological models have shown the importance of the diversity of potential hosts for understanding the dynamics of infectious disease (e.g., the importance of reservoirs), but the consequences of this diversity for virulence and transmission evolution remain largely overlooked. I will present a theoretical framework for the study of life-history evolution of multihost parasites. This analysis highlights the importance of epidemiology (the relative quality and quantity of different types of infected hosts) and between-trait constraints (both within and between different hosts) to parasite evolution. I illustrate these effects in different transmission scenarios under the simplifying assumption that parasites can infect only two types of hosts. I will also discuss situations where the system is far from its epidemiological equilibrium (e.g., just after the invasion of a novel host). These simple but contrasted evolutionary scenarios yield new insights into virulence evolution and the evolution of transmission routes among different hosts.

14-03 Talk

CORDYCEPS INFECTION OF ANTS IN A TROPICAL RAINFOREST: MUCH MORE THAN MEETS THE EYE.

David P. Hughes [1], Maj-Britt Pontopiddan [1], Nigel Hywel-Jones [2], Winanda Himaman [3], Boomsma J. Jacobus [1]

[1] *University of Copenhagen, Department of Biology, Universitetsparken 15, 2100, Copenahgen, Denmark*
[2] *BIOTEC, Mycology Department, Pathumthani, 12120, Bangkok, Thailand*
[3] *Dept of National Parks, Forest Entomology and Microbiology Group, 61 Phaholyothin Road Chatuchak, 10900, Bangkok, Thailand*

dphughes@bi.ku.dk

The parasitic fungus *Cordyceps* is well known because of its considerable medicinal importance and role in human culture. Its dramatic parasitism of ants, whereby infected individuals die in exposed places following adaptive manipulation of their behavior, means biologists are generally aware of it. Here we report that the apparent two player system (ant-*Cordyceps*) is a quinquepartite sub-foliar community comprising at least 25 species; most of which are specialized parasites of *Cordyceps*. We report of gall midges 'castrating' *Cordyceps,* dipteran and hymenopteran parasitoids attacking gall midges and a high diversity of hyperparasitic fungi attacking *Cordyceps*. Such a novel parasite community probably reflects the stable and long term occurrence of *Cordyceps* infected ants in tropical rainforests. We suggest that such heavy parasite pressure on *Cordyceps* feeds back upon its exploitation strategy of ants and we provide phenological evidence for this.

Also, utilizing a unique collection of infected ants amassed over a 17 year period we present molecular evidence of multiple host use by *Cordyceps unilateralis*, our principal parasite. Despite an ability to infect many ants its association with one principal host, *Camponotus leonardii,* probably reflects increased transmission success which may be traded-off against fitness losses due to its own parasite community.

High parasite biodiversity combined with a broad host range means *Cordyceps* presents a complex system underscoring the need to look beyond the classic host-parasite system that have informed our understanding thus far.

14-04 Talk

EVOLUTION AND DYNAMICS OF ONE PARASITE WITH MULTIPLE HOSTS: EPIDEMIOLOGY AND POPULATION GENETICS OF A TRYPANOSOMATID OF BUMBLE BEES

Mario X. Ruiz-González [1], Mark J. F. Brown [2]

[1] *Universidad de Valencia, Department of Genetics, Comparative Genomics, C/ Dr. Moliner 50, 46100, Valencia, Spain*
[2] *University of Dublin Trinity College, Department of Zoology, School of Natural Sciences, University of Dublin Trinity College, 2, Dublin, Ireland*

mario.x.ruiz@uv.es

The evolution of host-parasite interactions has been widely explored both theoretically and empirically, but the evolution and maintenance of the complex relationship of single parasite species with multiple host species remains relatively unstudied. We have examined the epidemiology and population dynamics of a trypanosome, *Crithidia bombi*, that parasitises multiple bumble bee host species. We used controlled laboratory infections to determine the population dynamics of interspecies parasite transmission, before examining the potential for such transmission in the field. *C. bombi* is transmitted via flowers, and we found that the pattern of flower use by foraging bumble bee hosts may lead to asymmetrical transmission of parasite strains among host species. Using microsatellites we then examined the population genetic structure of the parasite across species, locations and years. Patterns in parasite population structure appear to be driven by host species abundance and transmission dynamics. These data provide an insight into the dynamics, epidemiology and evolution of horizontally transmitted parasites with multiple host species.

14-05 Talk

IDENTIFYING MULTI-HOST SPECIES, A CRUCIAL STEP IN DETECTING HOST SHIFTS FROM COPHYLOGENY ANALYSES: THE CASE OF THE FUNGAL MICROBOTRYUM VIOLACEUM SPECIES COMPLEX

Guislaine Refrégier [1], Mickael Le Gac [1], Florian Jabbour [1], Jacqui A. Shykoff [1], Roxana Yockteng [1], Alex Widmer [2], Tatiana Giraud [1]

[1] *CNRS- University Paris-Sud, Ecological and Evolutive Genetics, Bat. 360, 91405, Orsay, France*
[2] *ETH Zürich, Institute of Integrative Biology, Bat. 360, 91405, Orsay, France*

guislaine.refregier@u-psud.fr

Microbotryum violaceum is a fungus that causes the sterilising anther-smut disease in many species of Caryophyllaceae. We constructed multiple gene phylogenies of smut strains from 21 host plants from different geographic origins, complementing a previous study on the delimitation of fungal species and of their host specificities. The smut phylogeny was then compared to that of their hosts. Both multi-host parasite species and multiple parasites on the same host were detected. Fine-scale congruence between the host and pathogen phylogenies was weak, frequent host shifts to moderately distant hosts appearing to be one of the dominating processes shaping evolutionary associations in this system. Genetics underlying the host-parasite interactions appeared to be an important factor influencing host-shifts and specialisation, as shown by the association of particular clades in the *Microbotryum* phylogeny with members of the same host clade and the fact that when a smut species was found parasitising several hosts then the host species were closely related. Because of this latter association pattern, when parasite species that infect multiple hosts were artificially duplicated in the phylogeny to have one branch per host species, the congruency was erroneously inflated. This shows the importance of carefully delimiting multi-host parasite species and their host specificities in cophylogeny studies.

14-06 Talk

PHYLOGENY AND GEOGRAPHY PREDICT PATHOGEN HOST RANGE IN WILD PRIMATES AND HUMANS

Amy B. Pedersen [1], T. Jonathan Davies [2]

[1] *University of Sheffield, Department of Plant and Animal Sciences, Alfred Denny Building, Western Bank, S10 2TN, Sheffield, UK*
[2] *National Center for Ecological Analysis and Synthesis, 735 State Street, 93101, Santa Barbara, USA*

a.pedersen@sheffield.ac.uk

Many of the most virulent emerging infectious diseases, e.g. AIDS and Ebola, are zoonotic – shifting from wildlife to humans. A critical question is what determines when and where a disease first crosses from one species to another. Using primates as a model, we show that infectious diseases are more often shared between species which are closely related and inhabit the same geographic region. A higher frequency of pathogen host shifts between close relatives and neighbours may explain this result. We find that host relatedness is the best overall predictor of whether two host species share the same pathogens. However, geographic overlap among neighbouring hosts is more important in determining host range for viruses. We suggest this is because rapid evolution within viral lineages allows host jumps across larger evolutionary distances. Our study is the first to demonstrate these relationships in a multi-host-multi-pathogen framework. We also show that the pattern of pathogen sharing with humans is the same as that between wild primates. For humans, this means we are more vulnerable to diseases from the great apes, including chimpanzees and gorillas; because these species represent our closest relatives. We translate our results into 'hotspot' maps, highlighting regions where the risk of disease transfer between wild primates and humans is greatest.

14-07 Talk

MODELLING THE EVOLUTIONARY IMPLICATIONS OF CONFLICT BETWEEN PARASITES WITH DIFFERENT TRANSMISSION MODES

Mike Boots [1]

[1] University of Sheffield, Animal and Plant Sciences, Western Bank, S102DR, Sheffield, UK

m.boots@sheffield.ac.uk

Most hosts are faced with a number of parasites that may cause powerful selective pressures on each other and their hosts. If the parasites have different life-histories and in particular if they have different transmission modes, there is the possibility of evolutionary conflict. Here I present an evolutionary game theoretical study that examines in general the evolutionary and coevolutionary implications of feminising vertically transmitted parasites (VTP) and horizontally transmitted parasites (HTP) sharing the same host. I also examine a detailed model of the evolutionary dynamics of the sabotage in a specific system. Our results emphasise that parasites can have important selective pressures on each other and that the outcome depends on the life-history of the parasites, and in particular the nature of the contraints between these and the characteristics of the host.

14-08 Talk

INTERACTIONS BETWEEN PARASITE DOSES AND THE HOST FOOD AVAILABILITY ON THE OUTCOME OF MOSQUITO COINFECTION BY TWO PARASITE SPECIES

Simon Fellous [1, 2], Claudy Haussy [1], Jacob C. Koella [2]

[1] Université Pierre et Marie Curie, Laboratoire de Parasitologie Evolutive, Quai St Bernard, 75005, Paris, France
[2] Imperial College London, Biology Division - Silwood Park Campus, Buckhurst road, SL5 7PY, Ascot, United Kingdom

simonfellous@free.fr

That many hosts are commonly infected by several species of parasites can strongly influence the epidemiology and evolution of parasites. We studied the combined effect of the microsporidium Vavraia culicis and the gregarine Ascogregarina culicis on their host, the mosquito Aedes aegypti. In particular, we investigated experimentally the effects on the host and the parasite traits of the doses of the two parasites and the availability of food to the mosquito larvae. In a full factorial design, we used two doses of each pathogen, as well as controls, and two food availability levels.

The host's age at pupation and emergence were controlled by the three-way interaction between parasitic doses and food availability: when food was scarce, pupation was delayed by one day if the doses of both parasites were high. There were fewer oocysts produced by A.culicis when the dose of V.culicis increased. In addition, challenging the hosts with the second parasite increased the proportion of these oocysts that were released locally (i.e. as the adult emerged, rather than elsewhere during oviposition). Similarly, the number of V.culicis spores depended on the interaction between food availability and exposure to A. culicis: it was lowered by coinfection, and even more with food deprivation.

Our results emphasize how interactions among environmental parameters can influence the effects of coinfection in unexpected ways. This may considerably affect ideas about the role of coinfections in the evolution of parasite virulence. Furthemore, as both parasites affected the other's transmission or development, there is potential for the interplay of their population dynamics.

14-09 Talk

CO-INFECTION WITH MICRO- AND MACROPARASITES: EVIDENCE OF INDIRECT INTERACTIONS AND A ROLE FOR TIMING?

Sandra Lass [1], Sarah Perkins [1], Peter Hudson [1]

[1] *The Pennsylvania State University, Dept. of Biology, Center for Infectious Disease Dynamics, 208 Mueller Lab, 16802, University Park, U.S.A.*

sandra.lass@psu.edu

There is growing interest in if and how other community members alter the ecological and evolutionary outcomes of pairwise interactions, such as between hosts and parasite. Simultaneous infections with more than one parasite species are common in natural host populations. Thus, the majority of host-parasite interactions do not evolve isolated but in a community context, and other parasites may affect the interaction directly and / or indirectly and alter disease dynamics in individual hosts and on the level of the host population. Furthermore, the timing of infection might be important and dynamics are likely to differ depending on which parasite species arrives first. Here, we test experimentally if co-infection with a macro- and a microparasite that do not share the same space in their host has consequences for the production of transmission stages and thus for the likelihood of transmission and virulence for each of both parasites. We use mice as model organisms and infect them either simultaneously or sequentially with a respiratory bacterium and a gastro-intestinal nematode. We hypothesize that both parasite species affect each other indirectly which may be mediated by the host's immune system. Furthermore, we hypothesize that these effects depend on which parasite establishes an infection first.

14-10 Talk

DYNAMICS AND EVOLUTION OF MULTIPLE INFECTIONS WITH VERTICALLY TRANSMITTED SYMBIONTS

Emilie Vautrin [1], Stéphane Genieys [2], Laurence Mouton [3], Sandrine Charles [1], Fabrice Vavre [1]

[1] *Université Claude Bernard Lyon 1, Laboratoire Biométrie et Biologie Evolutive, 43, bd du 11 Novembre 1918, Villeurbanne, France*
[2] *Université Claude Bernard Lyon 1, Institut Camille Jordan, 43, bd du 11 Novembre 1918, Villeurbanne, France*
[3] *Universität Basel, Zoologisches Institut, Basel, Switzerland*

vautrin@biomserv.univ-lyon1.fr

Associations between prokaryotic and eukaryotic individuals are widespread in nature and range from parasitism to mutualism. Frequently, several microorganisms simultaneously co-exist within a single host (co-infection). Within-host interactions affect the dynamics of the symbiotic population and therefore the co-evolution with the host.

Insect symbioses provide numerous examples of co-infections with vertically transmitted symbionts (from parents to offspring). Despite their high frequency, consequences of multiple infections on the evolution of the association have not been investigated. For a long time, such associations were thought to be rare because of a bottleneck occurring at each generation at the time of transmission, which leads to the genetic homogenization of the symbiotic population. However, active mechanisms can help stable maintenance of multiple infections along generations, creating privileged situations to study symbiont-symbiont interactions since vertical transmission locks the different partners together.

After a presentation of mechanisms that allow co-infections, we will use a mathematical model to study various scenarios for the evolution of conflict or cooperation between symbionts. Theoretical results suggest that cooperation between symbionts can be selected for in those symbioses and these results will be confronted with empirical data. Finally, as vertical transmission favours evolution towards mutualism because each partner relies on the others for successful reproduction, co-existence of vertically-transmitted symbionts could favour the emergence of cooperation.

14-01 Poster

VERY LOW DISPERSAL RANGE OF A TROPICAL TEPHRITINAE (DIPTERA: TEPHRITIDAE)

Aluana G. Abreu [1], Vera N. Solferini [1]

[1] *IB, Unicamp, Genética e Evolução, Cx. Postal 6109, 13083-970, Campinas, SP, Brazil*

agabreu@gmail.com

The flight range of small insects is very difficult to measure, leading to scarce information about their dispersal abilities. Generally, studies focus on economically important Tephritidae from temperate regions, but little is known about Neotropical non-frugivorous tephritids of subfamily Tephritinae. Temperate Tephritinae are fairly sedentary and short-lived, spending most of their whole life time on the host plants or in parts thereof. These low dispersal capacity would restrict gene flow between nearby populations, what should cause pronounced genetic differentiation. In this study, we investigated the genetic structure of a tropical tephritinae and compared it to what is expected for temperate flies. We studied 8 populations of *Tomoplagia reticulata,* distributed along Serra do Cipó in Brazil, using data from allozyme electrophoresis. *T. reticulata* parasitizes *Eremanthus glomerulatus* (Asteraceae), laying eggs in the flowerheads, where larvae develop. Allozyme variation indicated low gene flow, high levels of genetic differentiation within and between patches and high levels of inbreeding. These data suggest that there is really little dispersal of these flies. Besides their sedentary behavior, the small hills that separate patches may be acting as barriers to fly dispersal, contributing to the observed genetic structure. The low gene flow we report here is consistent with other studies, showing that both tropical and temperate Tephritinae flies have low dispersal rates.

14-02 Poster

NOVEL MARKERS FOR ASSESSING WOLBACHIA GENOME DYNAMICS IN THE CHERRY FRUIT FLY

Wolfgang Arthofer [1], Martin Krammer [2], Daniela Schneider [2], Markus Riegler [3], Christian Stauffer [1],
Wolfgang J. Miller [2]

[1] *University of Natural Resources and Applied Life Sciences, Institute of Forest Entomology, Forest Pathology and Forest Protection, Hasenauerstrasse 38, 1190, Vienna, Austria*
[2] *Medical University of Vienna, Centre of Anatomy and Cell Biology, Währinger Strasse 10, 1090, Vienna, Austria*
[3] *The University of Queensland, School of Integrative Biology, St. Lucia, QLD 4072, Brisbane, Australia*

wolfgang.arthofer@boku.ac.at

Wolbachia, infecting up to 76% of all insect species, is a powerful manipulator of host's reproduction causing effects like cytoplasmic incompatibility (CI). Today, most characterization approaches rely on the *wsp* surface protein gene.

The cherry fruit fly *Rhagoletis cerasi* shows crossing incompatibilities associated with an expanding *Wolbachia* double infection. We identified several *w*Cer strains in Sicilian populations. After transinfection into *Ceratitis capitata* and *Drosophila simulans* the high-level CI strain *w*Cer2 expresses high to intermediate CI in both heterologous systems. To avoid bias by co-transfer of other endosymbionts, systematic surveys on the microbial diversity of the *R. cerasi* germline are performed using the 16S rDNA locus. At least three *Wolbachia* strains infecting *Drosophila* species are identical to *w*Cer2 at the *wsp* sequence level but do not express CI in their natural hosts.

We identified three types of novel, polymorphic markers using the complete *w*Mel genome sequence: (i) variable tandem number repat loci (ii) the IS-5 transposable element, and (iii) ankyrin genes. We demonstrate that closely related *Wolbachia* strains differ significantly in these markers and report on the ongoing large screening of south-European *R. cerasi* populations.

14-03 Poster

INFECTION WITH AN ACANTHOCEPHALAN MANIPULATES AN AMPHIPOD'S REACTION TO A FISH PREDATOR'S ODOURS

Sebastian A. Baldauf [1], Timo Thuenken [1], Joachim G. Frommen [1], Theo C. M. Bakker [1], Oliver Heupel [1], Harald Kullmann [1]

[1] *University of Bonn, Institute for Evolutionary Biology and Ecology, An der Immenburg 1, 53121, Bonn, Germany*

sbaldauf@evolution.uni-bonn.de

Many parasites with complex life cycles increase the chances of reaching a final host by adapting strategies to manipulate their intermediate host's appearance, condition or behaviour. The acanthocephalan parasite Pomphorhynchus laevis uses freshwater amphipods as intermediate hosts before reaching sexual maturity in predatory fish. We performed a series of choice experiments with infected and uninfected Gammarus pulex in order to distinguish between the effects of visual and olfactory predator cues on parasite-induced changes in host behaviour. When both visual and olfactory cues, as well as only olfactory cues were offered, infected and uninfected G. pulex showed significantly different preferences for the predator or the non-predator side. Uninfected individuals significantly avoided predator odours while infected individuals significantly preferred the side with predator odours. When only visual contact with a predator was allowed, infected and uninfected gammarids behaved similarly and had no significant preference. Thus P. laevis increases its chance to reach a final host by olfactory-triggered manipulation of the anti-predator behaviour of its intermediate host.

14-04 Poster

MOLECULAR EVOLUTION OF PLANT GENES INVOLVED IN THE RECOGNITION OF SYMBIOTIC BACTERIAL PARTNERS: DANGEROUS LIAISONS WITH DISEASE RESISTANCE GENES ?

Thomas Bataillon [1], Stephane De Mita [2]

[1] *Genetics and Ecology, 8000C, AArhus, Denmark*
[2] *Wageningen University, Laboratory of Molecular Biology, Wageningen, The Netherlands*

tbata@daimi.au.dk

Plant genes involved in specific pathogen recognition (R genes) provide striking example of balancing polymorphism where variation is maintained by frequency dependent selection. In contrast virtually nothing is known about the expected evolutionary dynamics of genes involved in the recognition of symbiotic partners. An intimate association between legumes and soil bacteria, "rhizobia", leads to the development of root nodules inside which rhizobia trade fixed nitrogen for carbohydrates. This cross-kingdom collaboration exhibits strict host specificity controlled by the molecular structure of "Nod factors"released by rhizobia. Forward genetic strategies have recently identified plant genes that participate in Nod factor perception. Some of these genes bear a striking resemblance to known R genes families, suggesting that symbiotic recognition pahways have probably heavily recruted genes previously involved in pathogen recognition. We analyzed the patterns of nucleotide polymorphism of 24 independent anonymous loci and 5 genes intervening in Nod factor recognition in the legume *Medicago truncatula* in order to understand the selective forces shaping the evolution of these genes. We find that one recognition gene, *DMI1* which encodes a cation channel, shows the signatures of a putative selective event. In contrast, receptor-encoding genes *NFP* and *NORK* upstream of the recognition pathway show no signatures of selection in the recent history of *Medicago truncatula*.

14-05 Poster

EARLY PARASITE EXPOSURE AFFECTS SONG RATE OF MALE GREAT TITS

Linda L. Bischoff [1], Barbara Tschirren [2], Verena Saladin [1], Heinz Richner [1]

[1] *University of Bern, Zoology, Baltzerstrasse 6, 3012, Bern, Switzerland*
[2] *School of Biological, Earth and Environmental Sciences, NSW 2052, Sydney, Australia*

linda.bischoff@esh.unibe.ch

Bird song is a sexually selected trait known to contain honest information on current condition and health status of potential mates. It may, however, also contain information on past condition if the environment experienced early in life has long-lasting consequences on male vocalization (develomental stress hypothesis). Here we tested if a parasite infestation early in life affects the song rate or song repertoire (different song types) of adult great tits (Parus major). We exposed nestlings during growth to ectoparasitic hen fleas (Ceratophyllus gallinae) and, upon recruitment into the local breeding population the following year, measured their response to a playback of a challenging male in their breeding territory. Our results show that early parasite infestation affects adult song rate but not repertoire size. By assessing song rates during mate choice, females may thus gain information on early developmental conditions of potential partners.

14-06 Poster

WOLBACHIA DIVERSITY AND HOST SPECIALIZATION IN AN AFRICAN PARASITOID COTESIA SESAMIAE CAMERON (HYMENOPTERA:BRACONIDAE)

Antoine Branca [1], Stéphane Dupas [1], Bruno Le Rü [1], Jean-Francois Silvain [1]

[1] *IRD c/o CNRS, Biodiversity and Evolution of Plants - Insects Pests - Antagonists Complexes, Bat 13 1, avenue de la terrasse, 91198, Gif-sur-Yvette, France*

Antoine.Branca@legs.cnrs-gif.fr

Wolbachia are endocytoplasmic bacteria widely spread among arthropods. They are responsible, among other effects, for cytoplasmic incompatibility (CI) of gametes. Bidirectional CI (i.e. crosses between populations harbouring different Wolbachia strains are incompatible) has been shown to be an important mechanism in the early steps of speciation. The effect of Wolbachia on biological control agents has been studied in parasitoids only for the negative impact of Wolbachia invasion on the population dynamics. Their implication in adaptive differentiation and ecological speciation however has never been considered. In this study, we compare geographical distribution of virulence and Wolbachia strain diversity in Kenya for Cotesia sesamiae, an African stem borer parasitoid. For Wolbachia strain identification, we used molecular markers on four genes. Three strains were identified. PolyDNAviruses are symbionts implied in host immune response suppression. Individuals were genotyped therefore using a viral locus linked to virulence. Virulence distribution is highly congruent with Wolbachia and with the distribution on the main stemborer pest in the highland region, Busseola fusca Fuller (Lepidoptera: Noctuidae). The congruence between the distribution, the molecular divergence between Wolbachia strains and the absence of pre-zygotic isolation suggest that bidirectional CI is the main cohesive force in maintaining adapted populations. We explore this assumption theoretically by considering the relative influence of inbreeding and bidirectional CI level.

14-07 Poster

NO EVIDENCE FOR THE PRESENCE OF WOLBACHIA IN THE PARTHENOGENETIC INSECT SAGA PEDO

Josefa Cabrero [1], Ricardo Gómez [2], Juan Pedro M. Camacho [1]

[1] *Universidad de Granada, Departamento de Genética, Avda. Fuentenueva s/n, 18071, Granada, Spain*
[2] *Universidad de Castilla La Mancha, Departamento de CTA, E.T.S. de Ingenieros Agrónomos, 02071, Albacete, Spain*

jcabrero@ugr.es

The orthopteran insect *Saga pedo* is an all-female species with obligate apomictic parthenogenesis. Chromosome number is about twice that of its bisexual relatives, so it is apparently tetraploid. We analyse here the polyploid nature of this species and the possibility that its parthenogenetic reproductive mode is due to *Wolbachia* infection. For this purpose, we used several cytogenetic techniques and both standard and long PCR methods. Both ovary and gastric caeca cells showed 68 chromosomes grouped into 17 groups of four chromosomes with similar morphology and size, indicating the tetraploid nature of this species. C-banding showed the existence of large heterochromatic blocks in five chromosomes, and FISH showed that these blocks contain the ribosomal DNA. Finally, the two PCR methods employed failed to amplify the *Wolbachia* markers assayed, suggesting that parthenogenesis in *S. pedo* is not associated to the presence of this bacteria.

14-08 Poster

OUT OF THE PARENTS: GYNOGENETIC HYBRID LOACHES AVOID THE CONSTRAINTS OF SPERM-DEPENDENCY AND EXPAND BEYOND THE RANGES OF THEIR ORIGINAL SPERM-DONORS

Lukáš Choleva [1, 2], Apostolos Apostolou [3], M. Rábová [2], P. Ráb [2], Karel Janko [2]

[1] *Charles University in Prague, Faculty of Science, Department of Zoology, CZ-12843, Praha 2, Czech Republic*
[2] *Institute of Animal Physiology and Genetics AS CR ,v.v.i, Department of Vertebrate Evolutionary Biology and Genetics, Liběchov, CZ-27721, Czech Republic*
[3] *Bulgarian Academy of Sciences, Institute of Zoology, BG-10000, Sofia, Bulgaria*

lukas.choleva@biota.cz

Sperm-dependent parthenogens (gyno- and hybridogens) may be regarded as a special case of host-parasite systems, as such clonal populations, contrary to the true parthenogens, are reproductively dependent on sympatric bisexual species as a sperm-donor and decrease its reproductive potential via competition for sperm. Due to the requirement for sperm- and mating compatibilities, they rarely transcend the distribution ranges of the parental species. The scarce reports on gyno- and hybridogens occurring in the absence of parental populations do not identify the cause of such a pattern. We focus on the gynogenetic hybrid loaches (genus *Cobitis*) and show that the occurrences of two putatively ancient lineages outside the ranges of their parental species result from their dispersal into new areas rather than from outcompetition of parental taxa. Karyotype, allozyme and phylogeographic analyses suggest that both lineages arose in the lower Danube R. basin by the hybridisation of *C. elongatoides* with *C. tanaitica* or *C. taurica*, respectively. Both lineages subsequently dispersed as diploid F1's across whole distribution areas of parental taxa and invaded the range of neighbouring non-parental species, *C. taenia* in the Rhein R. and southern Ukraine. One lineage has further invaded the range of another, phylogenetically distant, loach species, *C. strumicae*. In both lineages, we found the evidence for repeated triploidisations via incorporations of the new host's chromosome set into the asexual genomes.

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14-09 Poster

PARASITIC IMMUNOSUPPRESSION: COSTS AND LOCAL ADAPTATION

Stéphane Cornet [1], Yannick Cornet [1]

[1] *Université de Bourgogne, UMR CNRS 5561 Biogéosciences, Ecologie Evolutive, 6 Bd Gabriel, 21000, Dijon, France*

stephane.cornet@u-bourgogne.fr

In host parasite systems, local adaptation of the parasite to the host may lead to adaptive parasitic alterations of the host phenotype in favour of the parasite fitness. Among these, parasitic down regulation of the host immune system may help the parasite to enhance its survival probability within the host body cavity, enabling the parasite to accomplish its life cycle. However, host immunosuppression may allow infections by opportunistic pathogens that will enhance death probability of the host and consequently prevent the former parasite to reproduce. Hence the parasite may have to balance its immunosuppressive effect according to the associated survival benefit and the indirect cost of killing its host. This is particularly the case for the acanthocephalan parasite *Pomphorhynchus laevis* that has a complex life cycle in which transmission from its intermediate gammarid host to its definitive fish host is achieved through predation. In Burgundy (eastern France), the local acanthocephalan parasite, *P. laevis* seems able to immunosuppress its local intermediate gammarid host, *Gammarus pulex*, but not the invasive one, *Gammarus roeseli.*

In this study, we characterised the effect of the acanthocephalan parasite on cellular and humoral parameters of the immune system of the both gammarid species. We further examined the efficiency of their immune system to clear an artificial bacterial infection when infected or not by the acanthocephalan parasite. We found that the infection of the local host by the acanthocephalan parasite is associated with lower levels of cellular and humoral immune defences and lower resistance to artificial bacterial infection. This phenomenon is not found in the invasive intermediate host. Our data suggest that parasitic immunosuppression results from co-evolutionary processes, which could come at a cost for the parasite by increasing host susceptibility to opportunistic pathogens that may enhance host death before the acanthocephalan transmission to the definitive host.

14-10 Poster

A FUNGAL ENDOPHYTE (EPICHLOE TYPHINA) CHANGES PALATABILITY OF ITS HOST GRASS PUCCINELLIA DISTANS

Marcin Czarnoleski [1], Pawel Olejniczak [2], Paulina Mikolajczak [3], Jan Kozlowski [1], Katarzyna Turnau [1], Dobroslawa Bialonska [1], Marlena Lembicz [3]

[1] *Jagiellonian University, Institute of Environmental Sciences, Gronostajowa 7, 30-387, Krakow, Poland*
[2] *Polish Academy od Sciences, Institute of Nature Conservation, Mickiewicza 33, 31-120, Krakow, Poland*
[3] *Adam Mickiewicz University, Institute of Environmental Biology, Umultowska 89, 61-485, Poznan, Poland*

czarn@eko.uj.edu.pl

Endophytic fungi are often considered to be beneficial for their host grasses because they are supposed to increase resistance to herbivores, pathogens and various abiotic stresses. Our work addressed the question whether infection with an endophytic fungus decreases susceptibility of grass seedlings to herbivory. In a lab experiment we compared the consumption of the grass *Puccinellia distans* infected and uninfected with the endophyte *Epichloe typhina* by the herbivory snails *Cepaea nemoralis*. We germinated seeds collected from grass populations with and without endophytic infections, and offered the two types of seedlings to starved snails. After 66 hours, freshly harvested seedlings were offered again. In the first experimental run, snails preferred endophyte-free to infected seedlings: consumption of infected biomass was ~ 20 % lower than the consumption of uninfected biomass. In the second run, consumption of both types of biomass heavily dropped and the preference for the endophyte-free seedlings was undetectable. We argue that endophytic fungi can significantly reduce vulnerability of grass seedlings to snail herbivory through production of chemicals decreasing palatability of a host species. We propose that this can explain why *Puccinellia distans* infected with the endophyte adopts a strategy of production of smaller seeds.

14-11 Poster

HOST-JUMPS BY MULTI-HOST PARASITE SPECIES CAN YIELD PHYLOGENIES AS CONGRUENT AS WOULD COSPECIATIONS

Damien M. De Vienne [1], Tatiana Giraud [1], Jacqui A. Shykoff [1]

[1] *Paris-Sud 11, Génétique et Ecologies Evolutives, Bât 360, 91405, Orsay, France*

damien.de-vienne@u-psud.fr

Congruence between host and parasite phylogenies is frequently observed in interacting host and parasite species. Such similarity between tree topologies is often taken as evidence for cospeciation of the hosts and their parasites. We simulated the adaptive radiation of a parasite on a new range of hosts with given phylogenies by jumping from one host to another and then speciating. We showed that the parasite and the host phylogenies were more congruent than expected by chance when the parasite was better at infecting hosts genetically close to the host they were already parasitizing. This congruence was greatly increased when adding the ability for the parasite to remain generalist for longer after jumps to closely related hosts than after jumps to more distant ones.

These results show the importance of estimating the ages of the nodes when studying host-parasite systems, as software classically used to infer host-parasite evolution with phylogenies can conclude to cospeciation where none occurred. The study further shows that the ability of parasites to infect multiple hosts has important consequences on the evolutionary pattern inferred through cophylogenetic analyses.

14-12 Poster

DO ENTOMOPATHOGENIC NEMATODES EXPERIENCE "SYMBIOTIC TRADE-OFF" BETWEEN SURVIVAL AND REPRODUCTION ?

Vanya Emelianoff [1], Elodie Chapuis [2], Nathalie Le Brun [1], Catherine Moulia [2], Jean-Baptiste Ferdy [2]

[1] *Université Montpellier 2, ISEM - CNRS UMR 5554, Place Eugène Bataillon, 34095, Montpellier, France*
[2] *Montpellier 2 university, ISEM, Place Eugene Bataillon, 34095 cedex 05, Montpellier, france*

vanya.emelianoff@gmail.com

Steinernema are nematodes which life cycle is divided in (i) a free stage, in the soil, where Infective Juveniles (IJs) of the nematode search for an insect host, and (ii) a parasitic stage where IJs penetrate the body of an insect host. In that second phase, IJs release bacteria they carry in their gut which kills the host, and reproduce to form new IJs. Previous studies clearly showed that IJs' success during the parasitic stage is increased when they carry their bacteria. Conversely, it has recently been shown that IJs mortality during the free stage was increased because of the bacteria. Those bacteria-linked costs and benefits could lead to trade-offs between life history traits of the symbiotic nematodes. We show that both IJs' parasitic success and mortality increase with the number of bacteria they carry. As a result IJs' survival negatively correlates with their parasitic success in the insect host when they carry bacteria. This correlation disappears when nematodes are deprived from their bacteria. This supports the symbiotic trade-off hypothesis. Such a trade-off might have a profound impact on the evolution of the symbiosis.

14-13 Poster

CO-INFECTION BY TWO MANIPULATING ACANTHOCEPHALAN PARASITES IN THEIR INTERMEDIATE HOST

Nathalie Franceschi [1], Alexandre Bauer [1], Loic Bollache [1], Thierry Rigaud [1]

[1] *Université de Bourgogne, UMR Biogéosciences, 6, boulevard Gabriel, 21000, Dijon, France*

nathalie.franceschi@u-bourgogne.fr

In Eastern French populations of the amphipod crustaceans *Gammarus pulex*, two species of acanthocephalan parasites coexist in sympatry: *Pomphorhynchus laevis* and *P. tereticollis*. These two complex life-cycle parasites use gammarids as intermediate hosts, and fish as final hosts. However, *P. laevis* uses preferentially chubs (*Leuciscus cephalus*) as definitive hosts, whereas *P. tereticollis* generally ends its life-cycle in barbels (*Barbus barbus*). These two fish species have different hunting strategies: barbels feed mostly on the bottom of the river, whereas chubs hunt in the river current. *P. laevis* and *P. tereticollis* are both able to manipulate the behaviour of their intermediate host, in a way that increases their trophic transmission to the definitive host. However, the levels of behavioural manipulation shown by naturally infected gammarids are different between the two *Pomphorhynchus* species, *P. laevis* inducing more pronounced alterations. This suggests that the parasites do not manipulate their intermediate hosts in the exactly same way, in order to be transmitted to the different fish species. The behaviour of gammarids simultaneously infected by the two parasite species remains uninvestigated. The parasites should be in conflict for their own transmission, to reach the “good” definitive host, a conflict that could be solved either by avoidance or sabotage of the manipulation. To investigate the result of such a co-infection, we therefore carried out controlled experimental infections of gammarids, followed by behavioural measurements.

14-14 Poster

A FLEA-INDUCED MATERNAL EFFECT MODULATES TICK FEEDING BEHAVIOUR ON GREAT TIT NESTLINGS

Katharina Gallizzi [1], Lise Gern [2], Heinz Richner [1]

[1] *University of Bern, Zoological Institute, Baltzerstr. 6, 3012, Bern, Switzerland*
[2] *University of Neuchâtel, Institute of Biology, Rue Emile-Argand 11, 2009, Neuchâtel, Switzerland*

katharina.gallizzi@esh.unibe.ch

A host's defence reaction against one parasite species can modulate the habitat quality for other parasites in both ways: It can either provide cross-resistance against closely related species due to antigenic similarity, or it can reduce resistance to other cohabiting species since the mounting of multiple defence reactions is more costly. Here we test for the first time whether parasites can also influence each other across host generations, that is, whether a hen flea induced maternal effect known to protect great tit nestlings against flea infestations will also alter tick feeding behaviour on nestlings. We infested half of the bird nests with fleas to induce the maternal effect and then cross-fostered nestlings to produce broods that contained both, nestlings with and without the flea-induced maternal effect. Five days after hatching we put 5 tick larvae on each nestling and assessed tick feeding behaviour. We found that ticks feeding on nestlings with the flea-induced maternal effect detached significantly earlier than ticks feeding on controls. It suggests that the flea-induced maternal effect alters tick feeding behaviour and that it may protect nestlings against tick borne diseases by reducing tick attachment times and thus the probability of pathogen transfer.

14-15 Poster

WHAT MAKES A SPIDER FLY? ENDOSYMBIONT INFECTIONS AND DISPERSAL

Sara L. Goodacre [1], Oliver Y. Martin [2], Linda Hutchings [3], Chris Woolley [3], Kamal Ibrahim [4], Godfrey M. Hewitt [5]

[1] *University of Nottingham, Institute of Genetics, Queen's Medical Centre, NG7 2UH, Nottingham, UK*
[2] *University of East Anglia, Centre for Ecology, Evolution and Conservation, NR4 7TJ, UK*
[3] *University of Plymouth, UK*
[4] *University of Illinois, Carbondale, USA*
[5] *University of East Anglia, Centre for Ecology, Evolution and Conservation, UK*

sara.goodacre@nottingham.ac.uk

Linyphiid spiders are abundant in heterogeneous landscapes, a fact that is attributed to their ability to re-colonize areas by wind assisted dispersal (ballooning using silk as sails). Becoming airborne requires the adoption of a dispersal-specific 'tiptoe' posture but individuals are unlikely to be able to control distance traveled once committed and this dispersal strategy thus carries the risk of mortality during the journey and of landing in unsuitable habitat. We have investigated the relationship between ballooning and infection with maternally inherited bacterial endosymbionts that are known to manipulate the reproduction of arthropod hosts. Spiders treated with antibiotics to remove endosymbionts were significantly more likely than their control counterparts to try to balloon, whilst other host traits considered were unaffected. Fewer infected individuals favored the risky dispersal strategy, which in turn is expected to reduce gene flow and to increase genetic isolation within the wider meta-population.

14-16 Poster

ANALYSIS OF THE GENETIC AND METABOLIC INTERACTIONS BETWEEN PRIMARY AND SECONDARY ENDOSYMBIONTS OF THE APHID CINARA CEDRI

María José Gosalbes [1], Javier Tamames [1], Araceli Lamelas [1], Andrés Moya [1], Amparo Latorre [1]

[1] *Universidad Valencia, Instituto Cavanilles de Biodiversidad y Biología evolutiva, Polígono de la Coma s/n, 46980, Paterna, Spain*

maria.jose.gosalbes@uv.es

Cinara Cedri is the aphid of cedar tree. Its diet is based on the phloem of the tree that is deficient in some nutrients as tryptophan and riboflavin. The insect bears two γ-proteobacteria: *Buchnera aphidicola*, BCc, primary endosymbiont, and *Candidatus* Serratia symbiotica (*Serratia symbiotica*), secondary endosymbiont. They are harboured in a protected environment in specialized cells called bacteriocytes.

Intracellular bacteria are characterized by genome reduction. The genome size of BCc is 422 Kb, approximately 200 Kb smaller than three previously sequenced *B. aphidicola* genomes The functional analysis of BCc indicates that it has lost its role in the mutualistic relationship, as it is not able to synthesize tryptophan and riboflavin, which should be supplied by another source, not only to the insect but alto to *Buchnera*. The secondary endosymbiont *Serratia symbiotica* has been proposed to carry out this role (Pérez-Brocal V. *et al*., 2006).

We are sequencing the whole genome of *S. symbiotica* using Genome Sequencer 20 (Roche Diagnostics) (Margulies M. *et al*., 2005). Preliminary results indicate that the genome has suffered a reduction in size, compared to the genome of free-living relatives. It shows also a low G+C content (around 30%). The characterization of its gene content shows that *S. symbiotica*, similarly to *B. aphidicola*, has lost the genes involved in DNA repair mechanisms, a feature related to the symbiotic process in other intracellular bacteria, although it retains other important determinants. Regarding its metabolic proposal role, it contains the genes involved in the riboflavin and tryptophan pathway. We discuss the results obtained on the light of the possibility that *B. aphidicola* BCc might be replaced by *Candidatus* Serratia symbiotica.

14-17 Poster

DETECTING SHIFTS OF TRANSMISSION AREAS IN AVIAN BLOOD PARASITES - A PHYLOGENETIC APPROACH

Olof Hellgren [1], Jonas Waldenström [2], Javier Peréz-Tris [3], Ezter Szöllısi [4], Dennis Hasselquist [1], Asta Krizanauskiene [5], Ulf Ottosson [6], Staffan Bensch [1]

[1] *Lund University, Department of animal ecology, Ecology Building, Sölvegatan 37, 22362, Lund, Sweden*
[2] *Kalmar University, Department of Biology and Environmental Sciences, 391 82, Kalmar, Sweden*
[3] *Universidad Complutense, Departamento de Zoología y Antropología Física, 28040, Madrid, Spain*
[4] *Eötvös Loránd University, Department of Systematic Zoology and Ecology, H-1117, Budapest, Hungary*
[5] *Vilnius university, Institute of Ecology, Vilnius, Lithuania*
[6] *A.P. Leventis Ornithological Research Institute, Jos university, Jos, Nigeria*

olof.hellgren@zooekol.lu.se

Avian blood parasites of the genera *Plasmodium*, *Haemoproteus* and *Leucocytozoon* exhibit large degrees of host-sharing and have the potential of conducting host-shifts over a large taxonomic range, thus having the potential of being transmitted between geographical distant areas and faunas with the help of migratory birds. However, of 259 different parasite lineages obtained from 5886 screened birds in Europe and Africa, only two lineages were confirmed to have current transmission in resident bird species in both geographical areas. We used a phylogenetic approach to show that parasites belonging to *Haemoproteus* and *Leucocytozoon* rarely change transmission area and that these parasites are restricted to one resident bird fauna over a long evolutionary time span and are not freely spread between the continents. Lineages of the genus *Plasmodium* seems more freely spread between the continents. We suggest that a reduced transmission barrier of *Plasmodium* parasites is caused by a higher tendency to infect migratory bird species, which might facilitate shifting of transmission area. Although parasites of these genera apparently shift between a tropical and temperate transmission area and these areas are linked with an immense amount of annual bird migration, our data suggest that novel introductions of these parasites into resident bird faunas are mainly to be considered as rare evolutionary events.

14-18 Poster

DISPERSAL AND PLANT SPECIFICITY IN THE GRAPEVINE YELLOWS "BOIS NOIR" VECTOR HYALESTHES OBSOLETUS (CIXIIDAE)

Jes Johannesen [1], Benjamin Lux [1], Kristina Michel [1], Alfred Seitz [1], Michael Maixner [2]

[1] *University of Mainz, Dept. Ecology, Saarstrasse 21, 55099, Mainz, Germany*
[2] *Federal Biological Research Centre for Agriculture and Forestry, Inst. Plant Protection in Viticulture, 54470, Bernkastel-Kues, Germany*

jesjo@uni-mainz.de

The grapevine yellows "bois noir" (BN) is one of the commercially most important diseases of wine in Europe. BN was first reported in Germany and France in the 1960's. Today, infection rates in some areas exceed 50%. Infection is caused by stolbur phytoplasmic bacteria that are transmitted by the planthopper *Hyalesthes obsoletus*. Wine is a dead-end host. Dead-end hosts are hosts that can be inoculated and subsequently become infested, but from which the vector can not acquire the pathogen. Infection usually represent a fitness loss to the dead-end hosts whereas transmission is fatal for the pathogen. Infections of wine (the dead-end host) can be viewed as an accidental side-effect of the vector's feeding behaviour. In Germany, the traditional host of the vector and reservoir plant, bindweed, has in the last ca. 15 yrs been replaced by stinging nettle as probably the most common host. The two plant species harbour different stolbur types (genotypes characterised by a RFLP restriction site in the elongation factor TU gene), which are also found in the emerging vectors. Hence, higher BN levels are related to a new host plant, high vector abundance on the new host plant and host-specific stolbur. In this paper, we consider the dispersal biology and local differentiation processes of *Hyalesthes obsoletus* at two levels: (1) by inferring historical dispersal of *H. obsoletus* we investigate whether the spread of disease in western Europe is related to range expansion of the vector and, more specifically, (2) we analyse whether the recent spread of BN in Germany is related to host races of *H. obsoletus* and, if true, whether host races in Germany originated locally or are immigrants from southern populations that traditionally use the new host plant.

14-19 Poster

DIVERGENCE IN HOST USE ABILITY OF A MARINE HERBIVORE AND ITS CORRELATES WITH HOST CHEMISTRY

Veijo Jormalainen [1], Outi Vesakoski [1], Riitta Koivikko [1], Jyrki Loponen [2], Vladimir Ossipov [2]

[1] *University of Turku, Section of Ecology, FIN-20014, Turku, Finland*
[2] *University of Turku, Department of Chemistry, FIN-20014, Turku, Finland*

veijo.jormalainen@utu.fi

Naturally fragmented distributions of the herbivore and its host plant assemblages are expected to lead to ecological divergence in the host use ability of the herbivore. Here we studied divergence of the host use ability in the isopod *Idotea baltica*, focusing to chemical correlates of the herbivore performance on its main host *Fucus vesiculosus*. Herbivore populations originating from two distinct plant assemblages, seagrass (*Zostera marina*) meadows vs. seaweed (*F. vesiculosus*) beds, performed superiorly on *F. vesiculosus*. Isopods from both the assemblages performed better on the sympatric than on allopatric host species, which indicates local adaptation. In a reciprocal feeding experiment among three populations from *F. vesiculosus* beds, we found the isopod populations being highly diverged in their host use ability. There was no general local adaptation but one of the populations performed better on the sympatric than on allopatric algae. When different *I. baltica* populations were fed with the same 30 *F. vesiculosus* genotypes, genetic variation in host quality was considerable. The performance of herbivores on distinct genotypes varied among the populations. Accordingly, the pattern of chemical correlates (determined by GC-MS of polar and lipophilic metabolites and HPLC of phenolics) of herbivore performance differed among the populations. The performance decreased with the total contents of phenolics. Thus, in this marine plant-herbivore system, local herbivore populations have diverged in their host use ability. This divergence includes local adaptation to utilize the sympatric host species of the plant assemblage. Host chemistry is crucial in the divergence and local adaptation of the host use ability.

14-20 Poster

ADAPTIVE RADIATION OF GALL-INDUCING INSECTS WITHIN A SINGLE HOST-PLANT SPECIES

Jeffrey B. Joy [1]

[1] *Simon Fraser University, Biological Sciences, 8888 University Drive, V55A 1S6, Burnaby, Canada*

jbjoy@sfu.ca

Speciation of plant-feeding insects is typically associated with host-plant shifts, with subsequent divergent selection and adaptation to the ecological conditions associated with the new plant. However, a few insect groups have undergone speciation while remaining on the same host plant species, and such radiations may provide novel insights into the causes of adaptive radiation. We used mitochondrial and nuclear DNA to infer a phylogeny for 14 species of gall-inducing Asphondylia flies (Diptera: Cecidomyiidae) found on Larrea tridentata (creosote bush), which have been considered to be monophyletic based on morphological evidence. Our phylogenetic analyses provide strong support for extensive within-host plant speciation in this group, and it demonstrates that diversification has involved numerous shifts between different plant organs (leaves, buds, flowers, and stems) of the same host-plant species. Within-plant speciation of Asphondylia is thus apparently facilitated by the opportunity to partition the plant ecologically. One clade exhibits temporal isolation among species, which may have facilitated divergence via allochronic shifts. The rate of change in an ecomorphological trait, ovipositor length, was significantly higher along branches with inferred shifts between host plant organs than along branches without such shifts. Population genetic data do not show strong spatial structure indicating high levels of gene flow across the range of the host plant. Taken together our results provide insight into the causes of diversity in phytophagous insects and into possible mechanisms of non-allopatric speciation.

14-21 Poster

MALE KILLING OR FEMINIZATION: WOLBACHIA CAN INTERFERE WITH THE SEX DETERMINATION OF INSECT HOSTS

Daisuke Kageyama [1], Satoko Narita [2]

[1] *NIAS, Insect-Microbe Research Unit, Owashi 1-2, 305-8634, Tsukuba, Ibaraki, Japan*
[2] *Chiba University, Faculty of Horticulture, 648, 271-8510, Matsudo, Chiba, Japan*

kagymad@affrc.go.jp

Wolbachia, a ubiquitous endosymbiotic bacterium that is inherited maternally in arthropod hosts, is maintained in host populations by exploiting various selfish strategies such as cytoplasmic incompatibility, parthenogenesis induction, male killing and feminization. In a moth, *Ostrinia scapulalis*, male offspring are selectively killed by *Wolbachia* (male killing), but the actual cause of the male killing is likely to be the feminizing effect of *Wolbachia*. *Wolbachia*-induced feminization, i.e., transformation of genetic males into functional females has been examined in a butterfly *Eurema hecabe*. We compare the similarities and differences of the *Wolbachia*-induced feminizing effects on these host species and try to integrate the fragmented knowledge on the mechanism of the seemingly distinct types of reproductive manipulation caused by the *Wolbachia* endosymbiont.

14-22 Poster

INVESTIGATION INTO THE HOST-PARASITE RELATIONSHIP OF SPHAERULARIA BOMBI AND ITS HOST(S) BOMBUS SPP.

Michael D. Kelly [1], Mark J. F. Brown [1]

[1] *Trinity College Dublin, Zoology, 2 College Green, D2, Dublin, Ireland*

kellym14@tcd.ie

The evolutionary ecology of parasites with multiple hosts is shaped by transmission among host species and species - species interactions. S*phaerularia bombi* (Nematoda, Tylenchida) is a parasite of bumble bee species. The adult parasite infects hibernating queens and upon their emergence castrates them and changes their behaviour to aid in dispersal of its of larvae. Larvae actively exit the host via the anus and are assumed to be deposited over the geographical range of the queen. However the rate of transmission among host species is not known due to possible host species-specific behaviours such as choice of hibernation site. Here we investigate indirect measures of species-specific host parasite interactions, including parasite distribution, reproduction and induced host mortality among host species. The parasite's prevalence in the Dublin area ranges from 0 to 50% with a prevalence of 46% in the most common host species, indicating asymmetries in the selection pressures felt by the host and the parasite across host species. Nevertheless, laboratory infections provide evidence, indicative of a generalist parasite. The temporal dynamics of prevalence and fecundity of the parasite were investigated in six host species with host longevity as a measure of virulence. These results shed light on the factors underlying host-parasite coevolution and virulence in single host and multiple parasite species systems.

14-23 Poster

MULTIPLE INFECTIONS, THEIR INFLUENCE ON THE SNAIL HOST AND EVOLUTIONARY CONSEQUENCES IN A TREMATODE/SNAIL SYSTEM

Kirsten Klappert [1], Jukka Jokela [1]

[1] *EAWAG, Aquatic Ecology, Ueberlandstrasse 133, 8600, Duebendorf, Switzerland*

kirsten.klappert@eawag.ch

Snail populations are commonly attacked by a community of trematode parasites. Inter- and intraspecific competition for hosts may be severe, and the theory predicts that this has consequences for the evolution of virulence. In many trematode species the larval stages have severe negative effects on host fitness and thus impose strong selection on their molluscan intermediate host. When multiply infected each of the parasites is expected to alter the host's phenotype/behaviour to their own advantage and interspecific conflicts among the parasites are expected to occur.

As some of the trematode species in a community are rare, very large datasets are required to examine the interactions between trematode species, i.e. the probability of specific species pairs co-occurring in the same host. Also, the life-cycles of the parasite differ with respect to definitive hosts and with respect to types of larval stages infecting the snails. Therefore, we can predict a dominance hierarchy of trematode species interactions. In an earlier study of digenetic trematodes in the freshwater snail *Potamopyrgous antipodarum* double infections were rare (only 0.6% of all analysed individuals), with the prevalence of double infections having been lower than expected by chance alone. Here we use a very large dataset (>50 000 snails) to investigate in more detail the type of antagonistic interactions among trematode parasite species in this New Zealand snail, and how these interactions relate to predictions of the theory.

14-24 Poster

DIPLOID AMAZON MOLLIES (POECILIA FORMOSA) OUTCOMPETE TRIPLOIDS IN CLONAL COMPETITION EXPERIMENTS

Dunja K. Lamatsch [1, 2], Kathrin P. Lampert [2], Petra Fischer [2], Matthias Geiger [3], Ingo Schlupp [4], Manfred Schartl [2]

[1] *University of Sheffield, Animal and Plant Sciences, Western Bank, S10 2TN, Sheffield, UK*
[2] *University of Wuerzburg, Physiological Chemistry I, Am Hubland, 97074, Wuerzburg, Germany*
[3] *MPIV Seewiesen, 82319, Starnberg, Germany*
[4] *University of Oklahoma, Zoology, 730 Van Vleet Oval, OK 73019, Norman, USA*

D.Lamatsch@sheffield.ac.uk

The sperm-dependent parthenogenetic Amazon molly (*Poecilia formosa*) is a mostly diploid species of hybrid origin. Triploids, however, occur in the Río Soto la Marina drainage in North-Eastern Mexico. It has been reported that triploids make up a variable but stable proportion of the unisexual population (approx. 5-15%). Assuming that allopolyploids may have an evolutionary advantage, i.e. being adapted to a wider range of environment than their diploid progenitors or showing sexual mimicry for their hosts, one should expect a selective sweep of triploids. On the other hand it could be costly to be triploid, e.g. it takes longer to duplicate the DNA at S phase for cell division, or maybe gene dosage effects might give rise to problems. Also larger genomes accumulate mutations faster.

The aim of our study was to show whether diploids or triploids have a selective advantage over the other biotype if competing under identical environmental conditions.

Diploids and triploids of equal number and size had to compete for sperm of two host males, *Poecilia mexicana limantouri* for 18 month (approx. 3-4 generations), monitored after 12 month.

Our results show that diploids clearly outcompeted the triploids in 5 of the 6 replicates showing the same tendency after 12 and 18 month. What stabilizes the triploid population in natural habitats will be subject of future studies.

14-25 Poster

A LONG-TERM RELATIONSHIP BETWEEN PRIMARY AND SECONDARY ENDOSYMBIONTS IN THE APHID CINARA CEDRI

Araceli Lamelas [1], Laura Gómez-Valero [1], Vicente Pérez-Brocal [1], Andres Moya [1], Amparo Latorre [1]

[1] *University of valencia, Institute Cavanilles, Polígono de la Coma s/n, 46980,, Paterna, Spain*

araceli.lamelas@uv.es

Bacterial symbioses are very abundant among insects, in which they are considered key to several specialized feeding behaviours and to their evolutionary diversification. Such associations are particularly widespread among members of the orders Homoptera such as aphids, whiteflies, psillids, or mealybubgs. One of the best known is the one stablished about 150 million years ago between aphids and *B. aphidicola*, their primary endosymbiont. Some aphids also harbor other bacteria, the secondary endosymbionts that are considered facultative. A particularly well described case is *B. aphidicola* BCc associated with the aphid *Cinara cedri*, member of the subfamily Lachninae with a genome size of 422 kb. The fact that it has lost most of the metabolic functions still retained in the others three *B. aphidicola* strains led us to postulate that *B. aphidicola* BCc is losing its symbiotic capacity and is being complemented (and might be replaced) by the highly abundant co-existing secondary symbiont *Candidatus* Serratia symbiotica (*S. symbiotica*) (Pérez- Brocal et al. 2006).

The aim of the present work is to shed light on the evolutionary process followed by the secondary symbionts that are present in species of the subfamily Lachninae and to determine whether *S. symbiotica* is well established in the subfamily, or the aphid *C. cedri* is just a particular case.

We carried out the sequencing and phylogenetic analysis of the ribosomal 16S gene of both symbionts in the same aphid, in representative species of the three tribes of the subfamily Lachninae. The obtained results suggest a long-time established relationship between the secondary endosymbiont and this subfamily of aphids. In addition, we postulate the presence of two types of *S. symbiotica* in different lineages. Finally, we performed electronic microscopy for morphologic analyses of both endosymbionts.

14-26 Poster

GENOME ANALYSIS OF THE OBLIGATORY COCKROACH ENDOSYMBIONT BLATTABACTERIUM SP.

María José J. López [1], Alexander Neef [1], Miguel Pignatelli [1], Javier Tamames [1], Amparo Latorre [1], Andrés Moya [1]

[1] *University of Valencia, Cavanilles Institute for Biodiversity and Evolutionary Biology, Polígono la coma s/n, 46980, Valencia, Spain*

maria.jose.lopez@uv.es

Cockroaches host in their abdominal fat body bacterial endosymbionts that are flavobacteria. Therefore, they belong to the phylum Bacteroidetes in contrast to all other insect endosymbionts so far genome-studied which are gamma-proteobacteria. Previously, we determined the size of the genome of the blattabacteria of *Blattella germanica*, *Periplaneta americana*, and *Blatta orientalis* as 650 +/- 15 kb indicating a reduced genome like it is typical for obligate endosymbionts.

We started a genome-sequencing project for the not culturable blattabacterial endosymbiont of *Blattella germanica* with the goals to learn about the specific adaptations that developed during the co-evolution 'blattabacteria – cockroach' in comparison to the gamma-proteobacterial endosymbionts as well as to reveal the so far unknown function(s) of the symbiont for the host via the annotation of the entire genome.

Up to now, we assembled 270 kb (40% of the genome size) in contigs. By BlastX searches we could identify in these stretches coding sequences for approximately 400 proteins. However, it turned out that up to 15% of the sequenced inserts stemmed from DNA from the host that was co-extracted as contamination. Additionally, due to the isolated phylogenetic position of the blattabacteria up to 40% of the raw sequences showed no homology at all to any entry in the NCBI-hosted data base. To overcome these specific drawbacks of our genome project we developed a set of bioinformatic tools for the pre-analysis of sequence reads like a categorizer based on examination of tetra- to heptamer frequencies and a pre-classification of sequences prior to assembly along quality criteria like BlastX match, categorizer score, DNA-G+C content, and contig length to optimize the assembly process.

14-27 Poster

AROMATIC PLANTS IN BLUE TIT (CYANISTES CAREULEUS) NESTS: A MULTIPLE-PARASITE DEFENCE?

Adèle Mennerat [1], Marcel M. Lambrechts [1], Philipp Heeb [2]

[1] *CEFE, CNRS, 1919 Route de Mende, 34293, Montpellier, France*
[2] *Université Paul Sabatier, Evolution et diversité Biologique, Bat 4R3, 31062, Toulouse, France*

adele.mennerat@cefe.cnrs.fr

Among birds, hole-nesters are exposed to a wide variety of parasites, from blood-sucking ectoparasites to pathogen endoparasites, bacteria or viruses. Many avian behavioural or physiological defence mechanisms against parasites are known, including specific (e.g. acquired immune system) and non-specific (e.g. preening) mechanisms. In Corsican natural populations, blue tit chicks are exposed to the highest levels of blood-sucking ectoparasitic blowflies (*Protocalliphora* sp.) reported in Europe. These ectoparasites can have severe negative effects on chick development and survival probabilities before fledging. Other blood-sucking insects, such as mosquitoes, are also found in nests. Corsican female blue tits (*Cyanistes caeruleus*) incorporate fresh fragments of a limited number of aromatic plants in the nest cup, from the end of the nest-building stage until the time chicks leave the nest. Some of these plants negatively affect bacterial growth and host location by blood-sucking mosquitoes in laboratory conditions. We investigated whether female blue tits bring aromatic plants to their nests as a defence against nest parasites. Here I will present our results and discuss the effects of plants on ectoparasite *Protocalliphora* blowflies, mosquitoes and nest bacterial communities in natural populations of Corsican blue tits.

14-28 Poster

INFLUENTIAL MICROBIAL GERM LINE SNEAKER: THE IMPACT OF WOLBACHIA ON DROSOPHILA EVOLUTION AND SPECIATION

Wolfgang J. Miller [1]

[1] *Medical University Vienna, Lab. Genome Dynamics, Center of Anatomy and Cell Biology, Waehringerstr. 10, A-1090, Vienna, Austria*

wolfgang.miller@meduniwien.ac.at

The intracellular alpha-proteobacteria Wolbachia is the most successful parasite of arthropods infecting up to 70% of all insect species. In some hosts these maternally transmitted bacteria are causing a diverse set of reproductive phenotypes such as cytoplasmic incompatibility (CI), male-killing, parthenogenesis, and feminization of genetic males.

Wolbachia infections targeting New World Drosophila species provide a unique opportunity for studying short- and long-term evolutionary host-parasite interactions. The comparative analyses of closely related Wolbachia infections in New World and Old World Drosophila hosts allow us to deepen our understanding in the diverse sets of conflict versus compromise strategies that have been evolved in different hosts over evolutionary time.

Based on our molecular, immunological and genetic data we will show that some long-term interactions have resulted in symbiotic strategies that (i) target the infection exclusively to the germ line, (ii) regulate the infection titer, and (iii) obviously play an important role in Drosophila speciation.

14-29 Poster

HOST BIOGEOGRAPHY MATTERS TO DECIPHER CO-DIFFERENTIATION WITH THEIR PARASITES

Caroline M. Nieberding [1, 2], Marie-Claude Durette-Desset [3], Alain Vanderpoorten [1], Juan Carlos Casanovas [4], Antonis Ribas [4], Valerie Deffontaine [1, 5], Carlos Feliu [4], Serge Morand [5], Roland Libois [1], Johan R. Michaux [1, 5]

[1] *University of Liège, B22, 4000 Sart Tilman, Belgium*
[2] *Leiden University, IBL, 2300 RA Leiden, The Netherlands*
[3] *MNHN, Laboratory of Systematics and Evolution, 75251 Paris, France*
[4] *Barcelona University, Laboratory of Parasitology, 08028 Barcelona, Spain*
[5] *Centre for Biology and Management of Populations, Campus Baillarguet, 34988 Montferrier-sur-Lez, France*

c.m.nieberding@biology.leidenuniv.nl

Long-term host-parasite interactions can involve the joint speciation of a host and its parasite[1]. We investigated if host speciation in the mouse genus *Apodemus* correlates with the diversification in the parasitic nematode genus *Heligmosomoides*. The mitochondrial *cyt b* gene was sequenced in 70 parasites sampled in the 6 *Apodemus* species. The ITS 1 and 2 of the 18S-26S nrDNA were also sequenced in 15 parasites to confirm the mitochondrial data. A single species of *Heligmosomoides,* namely *H. polygyrus,* was identified across the sampling of the 6 *Apodemus* species. This suggests that host speciation had no direct influence on parasite speciation, possibly due to frequent host-switches in the *Heligmosomoides* history. Within *H. polygyrus,* several lineages differentiated according to a geographic pattern. At a regional scale, the geographic distribution range of *H. polygyrus* lineages mirrors that of *A. sylvaticus* lineages in SW Europe, and that of *A. flavicollis* lineages in SE Europe. Thus, regional co-differentiation likely occurred between *H. polygyrus* and the two sister *Apodemus* hosts in different parts of their distribution range. We suggest that differences in past and present regional abundances of *A. sylvaticus* and *A. flavicollis* might be responsible for generating the pattern of regional co-differentiation. Conclusively, this study highlights that hosts biogeography matters to better understand their parasite phylogeography. [1]Nieberding CM, Olivieri I (2007) TREE **22**: 156-165.

14-30 Poster

PLOIDY, PARASITES AND DELETERIOUS MUTATIONS: INTERACTIONS INFLUENCING THE EVOLUTIONARY MAINTENANCE OF SEX

Andrew W. Park [1], Jukka Jokela [2], Yannis Michalakis [1]

[1] *IRD, Genetics & Evolution of Infectious Diseases, 911 Av Agropolis, 34394, Montpellier, France*
[2] *EAWAG, Aquatic Ecology, Überlandstrasse 133, 8600, Dübendorf, Switzerland*

andrew.park@mpl.ird.fr

The restrictive assumptions associated with purely genetic mechanisms (e.g. high genomic mutation rates; particular forms of epistasis) and purely ecological mechanisms (e.g. high parasite virulence / transmissibility) suggest that neither of the two forces, in isolation, can offer a general explanation for the evolutionary maintenance of sex.

Consequently, attention has turned to pluralistic theories. Naturally, modelling has attempted to gradually increase the level of complexity. Existing theory has shown that combining mutation accumulation and parasitism allows restrictive assumptions (about genetic and parasite parameter values) to be relaxed whilst still predicting the maintenance of sex. However, several empirical studies have shown that deleterious mutations and parasitism can reduce fitness to a greater extent than would be expected if the two acted independently. The implications of such interactions (with or without epistasis) are difficult to predict.

Our research is aimed at understanding how these genetic and ecological mechanisms interact in determining the fate of sex in both haploid and diploid hosts. Diploid hosts have received less attention and have the potential to behave differently to haploid hosts in respect to both host-parasite interactions (via infection genetics) and mutation accumulation (both at the individual and population level).

14-31 Poster

VIRUS-INDUCED BEHAVIOURAL MANIPULATION: A TRANSCRIPTOMIC APPROACH

Sabine Patot [1], David Lepetit [1], Delphine Charif [1], Julien Varaldi [1], Frédéric Fleury [1]

[1] *Université Claude Bernard, Lyon 1, Laboratoire Biométrie et Biologie Evolutive, UMR CNRS 5558, 43 boulevard du 11 Novembre 1918, 69622, Villeurbanne cedex, France*

patot@biomserv.univ-lyon1.fr

Viruses are usually considered to be infectious agents causing lethal or dramatic effects on their host. However, recent discoveries have revealed that lots of them are associated with much more discrete and subtle effects, and that they sometimes share some fitness components with their host due to vertical transmission. This type of virus is frequent in insects and is thus likely to play a major role on their evolution.

In *Leptopilina boulardi* (Hymenoptera: Eucoilidae), a solitary parasitoid of *Drosophila* larvae, some females are infected by viral particles (LbFV for *Leptopilina boulardi* Filamentous Virus) exhibiting both maternal and horizontal transmission. Females infected display a higher tendency to superparasitize (oviposit in a host already parasitized) than uninfected individuals, although only a single parasitoid larva can develop inside the host. The virus directly benefits from this behaviour since superparasitism conditions allow its horizontal transmission. This suggests that superparasitism behaviour may be the result of a manipulation of the parasitoid behaviour by this virus.

To identify candidate genes involved in the manipulation process, we used the Suppression Subtractive Hybridization (SSH) method in combination with Mirror Orientation Selection (MOS). This method allowed us to identify parasitoid genes that are deregulated by the virus together with potential virus genes. We will discuss the first results obtained with this approach.

14-32 Poster

EVOLUTIONARY IMPLICATIONS OF WITHIN-HOST SPECIATION OF MALARIA PARASITES

Javier Pérez-Tris [1], Staffan Bensch [2]

[1] *Universidad Complutense de Madrid, Departamento de Zoología y Antropología Física, 28040, Madrid, Spain*
[2] *Lund University, Department of Animal Ecology, 22362, Lund, Sweden*

jperez@bio.ucm.es

Cryptic parasite diversity (i.e. species diversity that cannot be uncovered using standard methods) may be an important characteristic in many host-parasite relationships, yet it is often neglected, either because it is difficult to deal with or just for the sake of simplicity. However, understanding cryptic parasite diversity may greatly improve our knowledge of the interactions between hosts and multiple species of parasites. In addition, cryptic parasite species are usually closely related, which makes them prone to exhibit complex evolutionary solutions to allow coexistence in the same host. Extreme cases of parasite cryptic diversity being boosted up in a single host species occur when parasites diverge from each other without switching hosts. Within-host speciation of malaria parasites has recently been discovered in *Haemoproteus* parasites of a passerine bird, the blackcap (*Sylvia atricapilla*). This discovery of within-host speciation changes our current view on the diversification potential of malaria parasites, because neither geographic isolation of host populations nor colonization of new host species are any longer necessary conditions to the formation of new parasite species. In addition, great parasite diversification occurred within blackcaps has led to variation in parasite transmission dynamics associated with variable host migratory behaviours. Such observations illustrate the importance of taking cryptic parasite diversity into account in studies of host-parasite evolution.

14-33 Poster

MICROSPORIDIAN PARASITE RADIATION IN BAIKALIAN AMPHIPODS

YANG QIU [1], Dimitry Sherbakov [2], Ravil M. Kamaltynov [2], Judith E. Smith [1]

[1] *Leeds University, Biology, Clarendon Way, LS2 9JT, Leeds, United Kingdom*
[2] *Siberian Branch of RAS, Limnological Institute, Ulanbatorskaja, 3, 664033, Irkutsk, Russia*

bgyyq@leeds.ac.uk

The diverse fauna of ancient lakes are often dominated by groups, which have undergone adaptive radiation to form species flocks. As species diversity, the potential for host pathogen interaction must increase, yet it is not known whether parasite species richness increases within rapidly evolving host species assemblages. Our study aims at testing whether adaptive radiation of free-living organisms is associated with the diversification of parasite species, based on cophylogenetic analysis.

Our study system is Lake Baikal in South Siberia, Russia, which is the oldest, deepest and one of the largest lakes in the world. Lake Baikal harbors more than 51 genera and 265 species of amphipods, which is a classic model of adaptive radiation. Up to date, we screened 20 species, 604 individuals of Baikalian amphipods, of which 13 species, 190 individuals were infected and 5 had dual infections. We have obtained 35 discrete microsporidian sequences, at least 23 speces of microsporidia in Baikalian amphipods. At least five groups of Baikalin microsporidia were monophyletic and sufficiently diverse to be considered as speices flocks. We conclude that microsporidia infecting Baikalian amphipods are very common and diverse. They are polyphyletic and might speciate by sympatric mechanisms.

14-34 Poster

EXPERIMENTALLY INCREASED GENETIC DIVERSITY IMPROVES DISEASE RESISTANCE IN ANT COLONIES

Anabelle Reber [1], Grégoire Castella [1], Philippe Christe [1], Michel Chapuisat [1]

[1] *University of Lausanne, Department of Ecology and Evolution, Biophore-Quartier Sorge, 1015, Lausanne, Switzerland*

anabelle.reber@unil.ch

A leading hypothesis linking parasites to social evolution is that genetically more diverse social groups better resist parasites. Here, we tested whether increased group diversity improved the resistance of the socially polymorphic ant Formica selysi to the virulent fungal parasite Metarhizium anisopliae. We first showed that matrilines varied in their resistance to the parasite. We then experimentally created three levels of group diversity by mixing matrilines. Workers in groups with higher diversity had slightly reduced survival in absence of infection. However, the pattern was reversed in the presence of the fungal infection: when challenged with Metarhizium, group diversity had a positive effect on worker survival. These results demonstrate that group diversity increases the mean resistance of group members to the parasite. Finally, groups of workers originating from single-queen colonies had a higher survival than groups of workers originating from multiple-queen colonies, both in controls and when challenged with Metarhizium, suggesting that natural variation in queen number correlates with variation in social, genetic and life history traits that have antagonistic effects on parasite resistance.

14-35 Poster

WOLBACHIA AND CARDINIUM INFECTIONS IN BRYOBIA MITES: THEIR EFFECTS AND INTERACTIONS IN ASEXUAL AND SEXUAL SPECIES.

Vera I. D. Ros [1], Johannes A. J. Breeuwer [1]

[1] *University of Amsterdam, Insitute for Biodiversity and Ecosystem Dynamics (IBED), Kruislaan 318, 1098 SM, Amsterdam, the Netherlands*

vidros@science.uva.nl

Wolbachia and *Cardinium* are two unrelated bacterial parasites capable of manipulating the reproductive system of their host species. Both bacteria are widespread in arthropods. Although these parasites are sometimes found to infect the same host species, their interactions have rarely been studied. We detected both bacteria in the mite genus *Bryobia*. This genus comprises over a hundred sexual and asexual species. We studied the distribution of the two parasites across these mite species and found single as well as multiple infections. *Wolbachia* are omnipresent in asexual species and antibiotic treatments confirm their role in causing the asexuality. In addition, *Wolbachia* is also infecting sexual species. *Cardinium* is less wide spread, but interestingly is co-infecting some sexual and asexual host species. Here we report on the results of crossing experiments in a sexual species, polymorphic for infection with W*olbachia* and *Cardinium*. Effects of both parasites and their interactions are discussed.

14-36 Poster

PATERNAL EFFECTS EXPLAIN SIGNIFICANT VARIATION IN RISK OF FUNGAL INFECTION IN FROG EGGS

Jörgen Sagvik [1], Tobias Uller [1], Mats Olsson [1]

[1] *Göteborg University, Zoology, Medicinaregatan 18, 413 90, Göteborg, Sweden*

jorgen.sagvik@zool.gu.se

Pathogens can have large impact on population dynamics via its effects on individual fitness. Documenting the sources of variation in host viability at pathogen exposure within and among populations is therefore important in order to predict host-pathogen evolutionary dynamics. Intraspecific variation in pathogen susceptibility in amphibians has previously not been addressed, and this may be a serious omission because potential variation in immunity is the raw material for natural selection and individuals and populations might have very different prospects of surviving pathogenic infection. We investigated family and population variation in the degree of embryonic infection of the pathogenic fungus *Saprolegnia spp.,* by infecting moor frog (*Rana arvalis*) eggs from six populations, and exposing them to two different temperatures. We found a significant family effect on the degree of *Saprolegnia*-infection of eggs and embryos. Furthermore, we found that the among-family variation in the infected eggs cannot be explained by maternal effects. Analyzed as a within-females effect, different sires gave rise to clutches that varied in their degree of infection, indicating genetic variation in resistance. Furthermore, relatively more eggs were infected when eggs were fertilized by sperm from the same, compared to a different, population. This effect was independent of variation in fertilization success. Thus, paternal effects explain significant variation in risk of fungal infection in frog eggs. We conclude that early developmental stages may show more diverse defences against pathogens than has previously been acknowledged.

14-37 Poster

DO HOST PLANT TOXINS PROTECT DROSOPHILA LARVAE FROM WASP PARASITISM?

Todd A. Schlenke [1], Neil Milan [1]

[1] *Emory University, Department of Biology, 1510 Clifton Road NE, RRC 1017, 30322, Atlanta, GA, USA*

tschlen@emory.edu

Drosophila species utilize a wide variety of host plants, many of which contain toxins. Certain fly species have evolved resistance to the toxins, and some have even evolved a preference for these toxins. Shifting to a normally toxic host plant may allow these species access to an underutilized food resource or may be a means of escaping parasitism. One possible example of the latter is the rarity with which cactophilic and fungivorous fly species are attacked by parasitic wasps. We set out to test 1) the level of resistance of various wasp parasitoids of Drosophila to toxins naturally found in Drosophila host plants, 2) whether parasitic wasps prefer to attack host larvae grown on standard Drosophila media as opposed to standard media supplemented with various natural plant toxins, 3) and whether wasp eggs are less likely to survive in Drosophila larval hosts grown on toxic media. The following combinations of flies and toxins are being tested: D. melanogaster grown on food containing ethanol, D. sechellia grown on food containing octanoic acid, and D. tripunctata grown on food containing alpha-amanitin. Among our preliminary results, we find that L. boulardi, a specialist parasitoid of D. melanogaster, is more resistant to ethanol knockdown than more generalist parasitoids. Furthermore, when given a choice between D. sechellia larvae growing on standard media versus media containing octanoic acid, L. boulardi females show strong avoidance of larvae grown on media containing octanoic acid.

14-38 Poster

ORIGINS OF SOCIAL PARASITISM: THE IMPORTANCE OF DIVERGENCE AGES IN PHYLOGENETIC STUDIES

Jaclyn A. Smith [1], Michael P. Schwarz [2]

[1] *Flinders University, School of Biological Sciences, GPO Box 2100, 5001, Adelaide, Australia*
[2] *Flinders University, Flinders University, GPO Box 2100, 5001, Adelaide, Australia*

jaclyn.smith@flinders.edu.au

Social parasitism is the relationship between two social insect species, where the parasite manipulates a host colony for its own benefit, but to the detriment of the hosts. Investigations of social parasitism have found sister-group relationships between the host and parasite species, and it has been suggested that these relationships indicate that these social parasites have evolved via sympatric speciation. All previous research has focused on ants, wasps and bumblebees, with social parasitism in allodapine bees having received very little attention. The lack of research is surprising because social parasitism has evolved more times in the allodapines than in all other bees and wasps combined, and has a higher proportion of social parasite species than any other social insect group. Each of the origins of social parasitism in the allodapines have varying divergence ages, ranging from relatively recent, to very ancient. Allodapine social parasites could consequently provide many unique insights into the processes that may have been involved in the evolution of a parasitic strategy. Numerous allodapine social parasites from Australia, Madagascar and Africa have been analysed using phylogenetic techniques, and seven independent origins have been found. These origins demonstrate different host-parasite relationships, which were found to correlate with the age of divergence of the parasites. We argue that our research highlights the caution that is needed when using phylogenetic techniques to determine species relationships, as such inferences can be problematic, as extinction, host switching and subsequent speciation, or an incomplete sampling of taxa could all confound the interpretation of phylogenetic relationships.

14-39 Poster

INTERSPECIFIC HOST DISCRIMINATION STRATEGIES IN A PARASITOID COMMUNITY

Joan Van Baaren [1], Cécile Le Lann [1], Jean-Sébastien Pierre [1], Liliane Krespi [2], Yannick Outreman [3]

[1] Université de Rennes 1, UMR ECOBIO, Campus de Beaulieu, av du Gal Leclerc, 35042, Rennes, France
[2] Université de Rennes 1, Ecologie des Insectes parasitoides, Campus de Beaulieu, av du Gal Leclerc, 35042, Rennes, France
[3] Agrocampus Rennes, UMR BIO3P, 65 rue de Saint-Brieuc, 35042, Rennes, France

joan.van-baaren@univ-rennes1.fr

Interspecific competition often occurs when several species share a common resource. In predators-prey systems, prey consumed by one species can not be available for the others, whilst in insect parasitoids, hosts already parasitized can be used by others as the parasitized host is still alive during parasitoid immature development. Thus, a single host can be attacked by several parasitoid species. However, multiparasitism (oviposition in a host already parasitized by another species) can be costly for solitary parasitoids as only one parasitoid can develop per host. To avoid fitness costs associated with multiparasitism, parasitoids should be able to recognise parasitism status of hosts they encounter. Such an ability, known as interspecific host discrimination, allows parasitoids to estimate the level of competition in a host patch and so to adjust their host use strategies accordingly. While intraspecific host discrimination has well been studied in parasitoids, studies on interspecific host discrimination are scarce, even though they are essential for understanding parasitoid community functioning. The aim of the present study was to analyse the interspecific host discrimination in a community of aphid parasitoids using a common host species. Results revealed that interspecific competition appears to have a high selective pressure as all species of this community are able to recognise hosts parasitized by others.

14-40 Poster

THE QUANTITATIVE GENETICS OF THE SUSCEPTIBILITY OF WHITEFISH EMBRYOS TO PSEUDOMONAS FLUORESCENS

Beat A. Von Siebenthal [1], Petra Kübele [1], Claus Wedekind [1]

[1] University of Lausanne, Department of Ecology and Evolution, Biophore, 1015, Lausanne, Switzerland

beat.vonsiebenthal@unil.ch

Empirical studies on the genetics or ecology of host-pathogen interactions are typically built on inferential statistics that require a sufficient number of independent replicates. This is why most progress in this field has been made with plants or invertebrates as model hosts. We established the methods to study host-pathogen interactions in fish embryos that are kept under semi-natural but very controlled conditions in thousands of independent replicates. We sampled a population of the Alpine whitefish Coregonus fera and used the gametes of 4 females and 12 males for in vitro fertilisation in a full-factorial breeding design („nested half-sib design“, i.e. all possible 48 sibships are produced). The embryos were reared in individual wells of cell-culture plates at standardised environmental conditions. We then exposed some embryos to the pathogen Pseudomonas fluorescens and sham-exposed others. Exposure to the pathogen induced precocious hatching and some embryo mortality. The study is nearly finished. We will quantify the additive and non-additive genetic variation, and the maternal environmental effects on embryo susceptibility or tolerance to the pathogen. These estimates of the variance components will contribute to the understanding of the genetics and evolution of this host-pathogen system.

14-41 Poster

GRASS ENDOPHYTES AND SUBARCTIC FINE FESCUES

Piippa R. Wäli [1]

[1] *University of Oulu, Department of Biology, University of Oulu, FIN-90014, Oulu, Finland*

piippa.wali@oulu.fi

Mutualistic symbionts may play an important role in performance and survival of plants. Seedborne systemic endophytic fungi of grasses are thought to be plant mutualists, because they have shown to improve host's resistance against herbivores and other biotic and abiotic stresses. The interactions in grass-endophyte associations vary from mutualistic to parasitic with environmental conditions and genotypes of interacting species (Saikkonen et al. 2004).

Occurence of *Epichloë fescue* endophyte in subarctic fine fescue populations differes among grass species and habitats (Wäli et al. 2007). Greenhouse experiment was conducted in order to examine if endophyte-infected and uninfected seeds and seedlings of two native grass species, *Festuca rubra* and *F. ovina*, differ in their seed germination and seedling growth. Also a two year greenhouse experiment of differing growing conditions with endophyte manipulated *F. ruba* half-sib families originating from two different habitats was carried out.

Seed family had marked effect on the seedling establishment of *F. rubra* and *F. ovina*. Costs of endophyte infection were detected in germination time and seedling performance of *F. ovina*. In *F. rubra,* the effects of endophyte on grass performance were dependent on the growing conditions and the original habitat in both experiments. The prevalence patterns of *E. fescue* as well as coevolution and interdependence between this seed transmitted symbiont and subarctic fine fescues are discussed.

Saikkonen, K. et al. 2004: Evolution of endophyte-plant symbioses. Trends in Plant Science. 9:275-280.

Wäli, P.R. etal. 2007: Occurrence and genetic structure of the systemic grass endophyte *Epichloë festucae* in fine fescue populations. Microbial Ecology 53:20-29.

14-42 Poster

ENDOPHYTES AND SUSCEPTIBILITY OF GRASSES TO FUNGAL PATHOGENS

Piippa R. Wäli [1]

[1] *University of Oulu, Department of Biology, University of Oulu, FIN-90014, Oulu, Finland*

piippa.wali@oulu.fi

Epichloë/*Neotyphodium* endophytes are suggested to be mutualistic symbionts of grasses. Most benefits of the endophyte infection in grasses are obtained by endophyte alkaloid-based herbivore defence. Endophytes can improve also the resistance or tolerance of host grasses to some pathogens or inhibit the colonization of mycorrhizal fungi (antagonistic interactions between the endophyte and other fungi), but in some cases endophytes are suggested to predispose the grasses to pathogenic fungi. The increased susceptibility of endophyte-infected grasses may occur via e.g. endophyte altered metabolism or the defence mechanisms of the host grasses.

Neotyphodium endophyte has been shown to increse the performance of meadow ryegrasses (*Lolium pratense*). In dual cultures *in vitro* meadow ryegrass endophyte had antifungal activities on two out of three winter pathogenic fungi tested. In the field experiment the endophyte-infected meadow ryegrasses were more susceptible to winter damages and *Typhula ishikariensis* pathogen than the endophyte-free grasses. There were differences in pathogenesis between the *T. ishikariensis* strains. Also, meadow ryegrass cultivar - endophyte status interaction were found in the growth of meadow ryegrasses. This highlights the effects of the genetic background of the participants on endophyte-grass-pathogen interactions. The endophyte effects on other interacting fungi may partly destabilize the mutualism between grasses and *Epichloë*/*Neotyphodium* endophytes.

14-43 Poster

PARASITE-MEDIATED COMPETITION AND OPTIMAL VIRULENCE

Thomas Zumbrunn [1], Dieter Ebert [1]

[1] *University of Basel, Institute of Zoology, Vesalgasse 1, 4051, Basel, Switzerland*

t.zumbrunn@unibas.ch

Complexity in host-parasite systems cannot only arise when single/multiple parasite species exploit multiple/single host species but also in cases where a parasite species exploits a host species which has to compete with a non-host species. The microsporidian parasite Octosporea bayeri is specialised in the cladoceran Daphnia magna which co-occurs with the non-host species D. longispina in metacommunities along the skerry island coast of southwest Finland. Mesocosm experiments have shown that O. bayeri infections reduce the competitivity of the host species and thus indirectly favour its competitor. Since an over-depletion of D. magna would eventually result in the displacement by D. longispina it is suggested that optimal virulence should stabilise at an intermediate level trading off parasite reproduction and interspecific competitivity of the host. Ongoing mesocosm experiments try to assess to what degree the observed virulence deviates from the predicted optimal virulence.

Social evolution in microbes and parasites

15

Thursday August 23 *Location*: Ekonomikum 1

Symposium 15: Social evolution in microbes and parasites

ORGANIZERS: Ashleigh Griffin, University of Edinburgh, UK
Sarah Reece, University of Edinburgh, UK

9.45-10.15	**Greg Velicer** (invited) The ecology of cooperation in microbes
10.15-10.45	**Angus Buckling** (invited) Siderophore-mediated cooperation and virulence in Pseudomonas aeruginosa
10.45-11.05	**Jacobus de Roode** Virulence and competition in genetically diverse malaria infections
11.05-11.35	*Coffee*
11.35-11.55	**Andy Gardner** Bacterial persistence is a social trait
11.55-12.15	**Michael Brockhurst** The ecology of cooperation in microbes
12.15-12.35	**Adin Ross-Gillespie** Frequency-dependence and density-dependence of cooperation in bacteria
12.35-12.55	**Kevin Foster** Cooperation and conflict in microbial biofilms: a story of slime, selfishness and suffocation
12.55-14.00	*Lunch*

15-01 Talk

TRACKING THE GENETIC BASIS OF EVOLVED SOCIAL STRATEGIES IN BACTERIA

Gregory J. Velicer [1]

[1] *Indiana University, Department of Biology, Bloomington, Indiana 47405, USA*

gvelicer@indiana.edu

Microbial systems and new sequencing technologies have opened new doors in the study of social evolution. Microbes allow documentation of rapid evolutionary changes in social behaviors and strategies, while sequencing of lab-evolved genomes allows characterization of the molecular basis of such change. Myxococcus xanthus is a highly social bacterium that engages in cooperative development of multicellular fruiting bodies upon starvation. Here I describe how a laboratory lineage of M. xanthus first evolved from a cooperative ancestral state into a cheating genotype that exploits its ancestor during development and then subsequently evolved back again to a novel state of cooperation. Sequencing the genome of the terminal evolved cooperator has provided initial insights in the molecular basis of these evolutionary changes in bacterial social behavior.

15-02 Talk

SIDEROPHORE-MEDIATED COOPERATION AND VIRULENCE IN PSEUDOMONAS AERUGINOSA

Angus Buckling [1]

[1] *University of Oxford, Department of Zoology, Oxford, OX1 3PS, UK*

angus.buckling@zoo.ox.ac.uk

Why should organisms cooperate with each other? Helping close relatives that are likely to share the same genes (kin selection) is one of explanation that is likely to apply across taxa. The production of metabolically costly extracellular iron-scavenging molecules (siderophores) by microbes is a cooperative behaviour because it benefits nearby conspecifics. I review experiments focusing on the production of the primary siderophore (pyoverdin) of the opportunistic bacterial pathogen, *Pseudomonas aeruginosa*, which test kin-selection theories that seek to explain the evolution of cooperation. First, cooperation is indeed favoured when individuals interact with their close relatives (both *in vitro* and *in vivo*); and when there is competition between groups of cooperators and non-cooperators, such that the benefit of cooperation can be realised. Second, elevated mutation rates can confer a selective disadvantage under conditions when cooperation is beneficial, because high mutation rates reduce how closely bacteria are related to each other. Third, cooperative pyoverdin production is also shown to be favoured by kin selection *in vivo* (caterpillars), and results in more virulent infections.

15-03 Talk

VIRULENCE AND COMPETITION IN GENETICALLY DIVERSE MALARIA INFECTIONS

Rustom Antia [1], Andrew Yates [1], Jacobus C. De Roode [2]

[1] Emory University, Department of Biology, GA 30322, Atlanta, USA
[2] University of Georgia, Institute of Ecology, GA 30602, Athens, USA

jaapderoode@hotmail.com

Humans and animals often become infected with different genotypes of the same parasite species, resulting in within-host competition between them. Much evolutionary theory has predicted that such competition should result in selection for higher virulence. This finding is based on the assumption that parasites with higher multiplication rates are both more competitive and virulent. Experiments with the rodent malaria *Plasmodium chabaudi* have shown that more virulent genotypes are indeed competitively superior, but that they do not have higher multiplication rates. We developed a mathematical model to describe these observed within-host dynamics of competing parasites in acute malaria infections. Our model incorporates haemeostatic regulation and an age structure of red blood cells, and shows that the competitive ability and virulence of malaria strains can be simply understood in terms of the age range of red blood cells they can infect. Thus, competition between malaria parasites during the acute phase of infection is governed entirely by resource competition for red blood cells, and is apparently unaffected by immunity. These results have important consequences for parasite evolution, supporting the hypothesis that resource competition between parasites selects for increased virulence.

15-04 Talk

BACTERIAL PERSISTENCE IS A SOCIAL TRAIT

Andy Gardner [1], Stuart A. West [1], Ashleigh S. Griffin [1]

[1] University of Edinburgh, Institute of Evolutionary Biology, King's Buildings
West Mains Road, Edinburgh, United Kingdom

andy.gardner@sjc.ox.ac.uk

The ability of bacteria to evolve resistance to antibiotics has been much reported in the media in recent years. It is less well-known that within populations of bacteria there are cells which are resistant due to a non-inherited phenotypic switch to a slow-growing state. Although such ‘persister’ cells are receiving increasing attention, the evolutionary forces involved have been relatively ignored. Persistence has a direct benefit to cells because it allows survival during catastrophes – a form of bet-hedging. However, persistence can also provide an indirect benefit to other individuals, because the reduced growth rate can reduce competition for limiting resources. This raises the possibility that persistence is a social trait, subject to the tragedy of the commons. Specifically, cells that allocate more time to the persister state could be out-competed by cells which allocate less time to the persister state, and instead invest more heavily in growth. We develop a theoretical model to investigate the social consequences of persistence. We predict that selection for persistence is increased when: (a) cells are related (e.g. a single, clonal lineage); and (b) resources are scarce. Our model allows us to predict how the level of persistence should vary with time, across populations, in response to intervention strategies and the level of competition. More generally, our results clarify the links between persistence and other bet-hedging or social behaviours.

15-05 Talk

THE ECOLOGY OF COOPERATION IN MICROBES

Michael A. Brockhurst [1]

[1] *University of Liverpool, School of Biological Sciences, Crown Street, L69 7ZB, Liverpool, UK*

michael.brockhurst@liv.ac.uk

Explaining social traits in microbes is a challenge. While kin selection provides a general explanation for the evolution of microbial social traits, we are far from understanding all the natural variation in microbial sociality. One reason for this is likely to be that extrinsic ecological parameters that are crucial for explaining patterns of diversity in nature remain largely unconsidered. Using an experimental evolution approach we have tested the role of disturbance, resource heterogeneity and resource supply in the de novo evolution of a cooperative trait, namely biofilm formation by the bacterium Pseudomonas fluorescens. Our results show that ecological conditions can have a significant effect on the evolution of cheats and has identified a range of ecological conditions most likely to favour the evolution of sociality in microbes.

15-06 Talk

FREQUENCY-DEPENDENCE AND DENSITY-DEPENDENCE OF COOPERATION IN BACTERIA

Adin Ross-Gillespie [1], Andy Gardner [2], Stuart A. West [1], Ashleigh S. Griffin [1]

[1] *University of Edinburgh, Institute of Evolutionary Biology, Ashworth Laboratories, Kings Buildings, West Mains Road, EH9 3JT, Edinburgh, United Kingdon*
[2] *Oxford University, St John's College, OX1 3JP, Oxford, United Kingdom*

a.ross-gillespie@ed.ac.uk

Microbes cooperate extensively in performing a wide range of multicellular activities, many of which are of profound medical or industrial importance. Hamilton's inclusive fitness theory provides a general framework by which to understand cooperation, but how well can standard models predict what happens in microbial systems? We conducted experiments with the pathogenic bacterium *Pseudomonas aeruginosa*, competing under various *in vitro* conditions strains that either produce (cooperate), or do not produce (cheat) an important but costly public good, *viz.* iron-scavenging siderophore molecules. We found clear negative frequency dependence: cheaters had a selective advantage when rare, but this declined when they were more common. Cheaters were also more detrimental to group-level productivity when common, although this effect was weakened when the period of population growth was experimentally shortened. We also found positive density-dependence: cheaters can only exploit cooperators if they are within the diffusion range of their siderophores, so the relative success of cheaters, when grown in the presence of cooperators, increases with population density. These results highlight the significance of frequency- and density-dependent feedback loops in the evolution of microbial cooperation. More generally, they demonstrate the importance of cheater-cooperator dynamics in microbial populations.

15-07 Talk

COOPERATION AND CONFLICT IN MICROBIAL BIOFILMS: A STORY OF SLIME, SELFISHNESS AND SUFFOCATION

Kevin R. Foster [1]

[1] *Harvard University, Center for Systems Biology, 7 Divinity Av, Bauer Labs, Room 104, 02138, Cambridge, MA, USA*

kfoster@cgr.harvard.edu

Sociobiology has come a long way. We now have a solid base of theory, centered on principles like inclusive-fitness theory and multilevel selection, and a myriad of empirical tests that support the theory's key tenets. One major group that remains largely unexplored, however, is the microbes, whose full spectrum of sociality only came to light in recent years. In particular, it has been realized that the dominant growth mode for many microbes is in large surface-attached communities known as biofilms, whose importance is underlined by their role in many chronic diseases, antibiotic resistance, biofouling and waste-water treatment. Our goal has been to investigate whether the classic theories of social evolution can be meaningfully and usefully applied to the biofilm phenotype. Using a combination of laboratory work with the pathogenic bacteria *Pseudomonas aeruginosa*, and individual-based simulations, we have investigated what happens when genetically-unrelated strains meet in biofilms. The outcome has been surprising: mixing strains tends to increase biofilm formation. This seems to run contrary to the classical theory, which predicts decreased sociality among non-relatives. We believe this to be solved by a simple switch in perspective, however. Biofilms are more driven by conflict, than cooperation.

15-01 Poster

NON-SELF VEGETATIVE FUSION AND GENETIC EXCHANGE IN ARBUSCULAR MYCORRHIZAL FUNGI

Daniel Croll [1], Alexander M. Koch [1], Ian R. Sanders [1]

[1] *University of Lausanne, Ecology & Evolution, Biophore, 1015, Lausanne, Switzerland*

daniel.croll@unil.ch

Arbuscular mycorrhizal fungi (AMF) form symbioses with the majority of plants, improving plant nutrition and promoting plant diversity. They form extensive underground hyphal networks simultaneously connecting the roots of different plant species. Network growth is thought to be entirely clonal and the fungi are considered to have been asexual for at least 400 million years. AMF individuals are multigenomic, containing populations of genetically different nuclei. Despite this unusual genome organization, knowledge of the genetics and mating systems of AMF is almost completely lacking. In filamentous fungi incompatibility mechanisms have evolved to prevent fusion of hyphae (anastomosis) among genetically different individuals, and, therefore, prevent genetic exchange. Here we present direct evidence that genetically distinct AMF, originating from the same population, anastomose resulting in viable cytoplasmic connections through which genetic exchange could occur. Using several molecular tools we show that genetic exchange indeed occurred between genetically different AMF. Specific genetic markers from each of two parents were transmitted to the spores (progeny) and these spores were viable, forming symbioses with plant roots. The ability to experimentally perform genetic crosses among AMF lays a foundation for understanding the evolutionary biology of these important plant symbionts and investigate the conditions for co-existence of multiple genomes within an organism.

15-02 Poster

FAMILY-BASED GUILDS IN ANT SOCIETIES

Patrizia D'Ettorre [1], Oliver Aehle [1], Maurice Roux [2]

[1] *University of Copenhagen, Population Biology, Universitetsparken 15, 2200, Copenhagen, Denmark*
[2] *University Marseille III, Marseille, France*

pdettorre@bi.ku.dk

Medieval organization of human societies in Europe depended on guilds of artisans that were partly heritable, but the stability of guild-based economies also required central regulation to suppress competitive and nepotistic tendencies (ref). Here we document that ponerine ants have division of labor that allows heritable task specialization to be expressed while controlling for the potentially damaging consequences of reproductive competition by centralized breeding. When offered multiple nest cavities, workers of *Pachycondyla inversa* distributed themselves in full sister groups characterized by specific cuticular hydrocarbon profiles and inherent tendencies to engage in different tasks. The unrelated mother queens, however, stayed together in a single nest chamber with most of the brood. Social cohesion thus depends on established dominance hierarchies among queens and the joint complementary efforts of worker guilds, whereas disruptive tendencies are avoided because kin discrimination is not enhanced by the interference of workers.

15-03 Poster

THE ROLE OF RELATEDNESS IN THE SUCCESS OF CHEATER STRATEGIES IN THE SOCIAL AMOEBA DICTYOSTELIUM DISCOIDEUM

Ana Duarte [1], Gerda Saxer [2], Lorenzo Santorelli [2], Adam Kuspa [3], Gad Shaulsky [4], David C. Queller [2], Joan E. Strassmann [2]

[1] *University of Groningen, Theoretical Biology Group, P.O. Box 14, 9750 AA, Haren, The Netherlands*
[2] *Rice University, Department of Ecology and Evolutionary Biology, 6100 Main Street, 77005, Houston, Texas, U.S.A.*
[3] *Baylor College of Medicine, Department of Biochemistry and Molecular Biology, One Baylor Plaza T321, 77030, Houston, Texas, U.S.A.*
[4] *Baylor College of Medicine, Department of Molecular and Human Genetics, One Baylor Plaza T321, 77030, Houston, Texas, U.S.A.*

A.L.F.Duarte@rug.nl

According to kin selection theory, altruistic behavior can be explained through high relatedness between coooperating individuals. At low levels of relatedness, there may be selection for cheating behavior, thus threatening the stability of cooperation. In aggregates of *Dictyostelium discoideum*, a social amoeba, some cells behave altruistically by dying to form a stalk that holds aloft a sorus with fertile spores. Different clones join these aggregates, which can lead to conflict over who contributes more spores. We generated cheater clones by knocking out individual genes, and then selecting for success in becoming spores. In this study we tested 8 of these mutants at high and low relatedness conditions, predicting that the mutants would increase in frequency more in high relatedness than in low relatedness conditions. We found that cheaters increased under both high and low relatedness conditions. A possible explanation for the observed pattern is that the mutants also have non-social advantages. Future work will increase the precision of the success measure, and will look for advantages to the mutants at other stages in the life cycle. Clearly social amoebae hold great promise as model organisms for studying social evolution.

15-04 Poster

EVOLUTION, ECOLOGY AND PATHOLOGY OF SIDEROPHORE COOPERATION IN PSEUDOMONAS AERUGINOSA.

Freya Harrison [1], Angus Buckling [2]

[1] University of Oxford, Department of Zoology, South Parks Road, OX1 3PS, Oxford, UK
[2] University of Oxford, Department of Zoology, South Parks Road, OX4 1SP, Oxford, UK

freya.harrison@zoo.ox.ac.uk

Siderophore production by the opportunistic animal pathogen P. aeruginosa is an excellent model system for exploring the ecology and evolution of cooperation, and also allows direct inferences about the links between cooperation and virulence to made. We have used this system to explore a) how relatedness affects pathogen virulence, b) how the evolution of high mutation rates affects cooperation (and vice versa) and c) how interspecific interactions can affect intraspecific cooperative behaviour. Our results begin to shed light on the possible links between community structure, abiotic environmental conditions, evolutionary change and levels of cooperation. We attempt to interpret our results in clinical terms, specifically with reference to chronic lung infections of cystic fibrosis patients.

15-05 Poster

HIGH DELETERIOUS GENOMIC MUTATION RATES IN STATIONARY PHASE MAY FORCE COOPERATION

Laurence Loewe [1]

[1] University of Edinburgh, Institute of Evolutionary Biology, Ashworth Labs, Kings Bldgs, W Mains Rd, EH9 3JT, Edinburgh, Scotland, UK

Laurence.Loewe@evolutionary-research.net

In natural habitats, bacteria spend most of their time in some form of growth arrest. Little is known about deleterious mutations in such stages, and consequently there is limited understanding of what evolutionary events occur. In a deleterious mutation accumulation experiment in prolonged stationary phase of Escherichia coli, about 0.03 slightly deleterious mutations were observed per genome per day. This is over an order of magnitude higher than extrapolations from fast-growing cells, but in line with inferences from observations in adaptive stationary phase mutation experiments.
The resulting speed of mutation accumulation makes it difficult for a subpopulation of adapting cells to survive extended periods of stationary phase without loosing at least some functions needed for exponential growth. Since not all cells in stationary phase become transient hypermutators, functional sets of genes that are needed for exponential growth remain physically close, even if the nonmutators that carried them are no longer alive.
If there is some recombination like e.g. transformation, a particular type of cooperation can occur: Nonmutators preserve adaptations to the old environment at the risk of dying in the new, while mutators explore new adaptations at the expense of damaging good genes. If mutators survive by adapting to a big environmental change, then (i) the well-preserved house-keeping genes of nonmutators may help repair mutational damage in the surviving mutators or (ii) surviving nonmutators may pick up new adaptations from mutators that help them grow faster. The result is a more powerful system of microbial evolution. These findings may affect understanding of bacterial evolution and the emergence of bacterial pathogenicity.

15-06 Poster

ADAPTATION OF A SIMPLE MULTI-CELLULAR ORGANISM TO A NOVEL ENVIRONMENT

Bart P. S. Nieuwenhuis [1], Marijke Slakhorst [1], Alfons J. M. Debets [1], J Arjan G. M. De Visser [1]

[1] *Wageningen University, Evolutionary Genetics, Arboretumlaan 4, 6703 BD, Wageningen, The Netherlands*

bart.nieuwenhuis@wur.nl

Experimental evolution has generated many insights in the process of adaptation, but usually uses simple, single-celled organisms. We have investigated adaptation in a simple multi-cellular organism, by allowing 18 replicate lines of the filamentous fungus *Aspergillus nidulans* to undergo asexual adaptation to a novel environment. Competitive fitness and four fitness components were measured after adaptation for 0, ~300 and ~600 cell doublings. An average fitness increase of 36% and 96% was found for the later two time points, respectively. No deceleration in adaptation was found. Germination speed, mycelial growth and size and yield of asexual spores were measured to gain insight in the contribution of these life history changes to adaptation. Delayed germination and increased mycelial growth were correlated with fitness, but spore size or yield was not correlated. Reduced germination speed, which was expected to reduce fitness, is probably a negatively pleiotropic effect of increased mycelial growth rate. Correlations between changes in fitness and in a component found at one time-point but not at the other, suggest that changes in different components are associated with fitness effects of different size, or that positive effects contributed by components sometimes epistatically depend on earlier changes in other components.

15-07 Poster

ISOLATION BY DISTANCE IN THE SPORE-FORMING SOIL BACTERIUM MYXOCOCCUS XANTHUS

Michiel Vos [1], Gregory J. Velicer [2]

[1] *University of Oxford, Zoology, Tinbergen Building South Parks Road, OX1 3PS, Oxford, U.K.*
[2] *Indiana University, Biology, A400 Jordan Hall, 47405, Bloomington, USA*

michiel.vos@zoo.ox.ac.uk

Very little is known about the degree to which populations of free-living prokaryotes are spatially structured. *Myxococcus xanthus* is a globally distributed spore-forming bacterium that offers a robust test for genetic differentiation among populations since sporulation is expected to enhance dispersal. Using multi locus sequence data, we show that *M. xanthus* populations are genetically distinct at scales exceeding 10^2 – 10^3 km and that isolation by distance, the divergence of populations by genetic drift due to limited dispersal, is at least partly responsible. This is the first explicit demonstration of population structure in a free-living soil bacterium with a contiguous habitat.

Cytonuclear coevolution and the evolution of hybrid zones

16

Saturday August 25 *Location*: Ekonomikum 1

Symposium 16: Cytonuclear coevolution and the evolution of hybrid zones

ORGANIZERS: Johan Lindell, University of Toronto, Canada
Staffan Bensch, Lund University, Sweden

9.45-10.15	**David Rand** (invited) Mitonuclear coadaptation, epistasis and fitness
10.15-10.45	**Ronald Burton** (invited) The role of nuclear/mitochondrial genome incompatibility in interpopulation hybrid breakdown
10.45-11.05	**Damian Dowling** Cytonuclear coevolution and the effects of cytonuclear disruption on hybrid viability in a seed beetle
11.05-11.35	*Coffee*
11.35-11.55	**Oliver Niehuis** Cytonuclear genic incompatibilities in hybrids of Nasonia parasitoid wasps
11.55-12.15	**Laurene Gay** Detecting cytonuclear conflicts by comparing introgression rates between mitochondrial and nuclear DNA in two zones of secondary contact between large gulls.
12.15-12.35	**Andreia Miraldo** Mitochondrial DNA heteroplasmy and recombination in a reptilian secondary contact zone
12.35-12.55	**Jacek Szymura** Can negative cytonuclear interactions explain mtDNA patterns in Bombina hybrid zones?
12.55-14.00	*Lunch*

16-01 Talk

MITONUCLEAR COADAPTATION, EPISTASIS AND FITNESS

D. M. Rand [1], C. Meiklejohn [1], K. Montooth [1], R. Haney [1], J. Hofmann [1], R. Wagaman [1]

[1] *Brown University, Ecology and Evolutionary Biology, Providence RI, US*

David_Rand@brown.edu

In addition to their insight into speciation, hybrid zones provide an excellent opportunity to study the genetic interactions that govern nuclear-mitochondrial (mitonuclear) fitness effects in the nature. Joint analyses of mitochondrial and nuclear genes are a standard means of dissecting the genetic architecture of hybrid zones. Early studies suggested that mtDNA crosses species boundaries more easily than nuclear loci, but this generality may not hold in all cases. Normal eukaryotic activity requires coordinated expression of nuclear and mitochondrial genes, thus mitonuclear epistatic interactions are a nice model system for studying coadapted genome complexes. We examine this question at several levels. First, we provide a molecular evolutionary analysis of the nuclear and mitochondrial proteins comprising the enzyme complexes of oxidative phosphorylation (OXPHOS) in the recently sequenced Drosophila genomes. These data reveal distinct patterns of gene- and lineage-specific positive and negative selection in both nuclear and mtDNA encoded proteins. Second, we examine mitochondrial enzyme activity and metabolic performance of introgression strains between *D. melanogaster* and *D. simulans* where alternative mtDNAs are carried on distinct nuclear chromosomal backgrounds. We test two hypotheses: 1) that mito-nuclear disruption scales with degree of genetic divergence between subunits, and 2) whether the sexes differ in their disruption of mitochondrial phenotypes in these introgression strains, as predicted from maternal inheritance and the evolution of modifiers. Finally, we describe fitness assays of experimental hybrid zones where *D. melanogaster* and *D. simulans* mtDNA compete. Population cage experiments, desiccation, and locomotor activities indicate that the fitness effects of mtDNA haplotypes are modified by specific chromosomal backgrounds. These mitonuclear epistatic interactions are further altered by dietary conditions. We discuss strategies for identifying these nuclear modifier loci of mitochondrial function, and argue that hybrid zones could be a great system for finding such loci in nature.

16-02 Talk

THE ROLE OF NUCLEAR/MITOCHONDRIAL GENOME INCOMPATIBILITY IN INTERPOPULATION HYBRID BREAKDOWN

Ronald S. Burton [1], Christopher K. Ellison [1]

[1] *University of California, San Diego, Marine Biology Research Division, Scripps Institution of Oceanography, 92093-0202, La Jolla, CA, USA*

rburton@ucsd.edu

Genetic divergence between allopatric populations can ultimately lead to reproductive isolation and speciation; hybrid breakdown represents an early stage in this differentiation, when interpopulation hybrids exhibit reduced fitness. Where hybrid breakdown occurs only in the F_2 and later generations, genetic incompatibilities between populations typically involve interlocus interactions, commonly referred to as Dobzhansky-Muller incompatibilities. The potential role of mitochondrial genomes (mtDNA) in these interactions has not been widely examined because few genes are encoded in the mtDNA and some studies have indicated that mtDNAs are compatible across sister taxa. However, recent experiments have shown that nuclear/mitochondrial incompatibilities are in fact the primary cause of reduced fitness in interpopulation hybrids of a marine copepod, Tigriopus californicus. The role of the mitochondrial genome was tested by backcrossing low fitness F_3 hybrid females to males from either the maternal or the paternal parental population. In all cases, offspring from maternal backcrosses exhibited completely restored fitness, whereas offspring from paternal backcrosses showed no evidence of fitness recovery. Investigations of the molecular mechanisms that may underlie nuclear/mitochondrial incompatibility in T. californicus hybrids will be presented.

16-03 Talk

CYTONUCLEAR COEVOLUTION AND THE EFFECTS OF CYTONUCLEAR DISRUPTION ON HYBRID VIABILITY IN A SEED BEETLE

Damian K. Dowling [1], Urban Friberg [1], Katia Chávez Abiega [1], Albert Larkeson Nowostawski [1], Göran Arnqvist [1]

[1] *Uppsala University, Animal Ecology / Dept. Ecology & Evolution, EBC, Norbyvägen 18D, 75236, Uppsala, Sweden*

damian.dowling@ebc.uu.se

The interaction between the mitochondrial and nuclear genomes coordinates energy production and should be under strong selection. Indeed, several studies have now found that mitochondrial genes commonly have effects on fitness, with these effects primarily manifested via cytonuclear interactions at a between-population level. Such findings are intriguing since they imply that disruption of coadapted cytonuclear gene complexes will lead to functional incompatibilities that result in hybrid breakdown. If so, then cytonuclear fitness interactions may constitute a driving force for reproductive isolation between populations. In addition, recent evidence suggests that post-copulatory processes, namely sperm competition and cryptic female choice, are fundamental contributors to the evolution of reproductive isolation. Here we test for cytonuclear interactions on several fitness traits (development time, female remate rates, sperm viability, sperm length and sperm competitive success), several of which are likely shaped by post-copulatory sexual selection. We then examine whether disruption of the coadapted cytonuclear gene complexes results in reduced performance in these traits. This was achieved using introgressive backcrossing to generate lines of seed beetles (*C. maculatus*) carrying orthogonal combinations of distinct cytoplasmic and nuclear lineages sampled from allopatric populations. We found cytonuclear effects on development time, sperm viability and length. Further, disruption of the coevolved cytonuclear combinations consistently resulted in altered performance in each of these traits. In the case of the sperm traits, performance clearly declined post-disruption. These findings have profound implications because they suggest that cytonuclear fitness interactions are not only ubiquitous, but could impose a powerful isolating mechanism when allopatric populations establish secondary contact.

16-04 Talk

CYTONUCLEAR GENIC INCOMPATIBILITIES IN HYBRIDS OF NASONIA PARASITOID WASPS

Oliver Niehuis [1], Jürgen Gadau [1]

[1] *Arizona State University, School of Life Sciences, PO Box 874501, 85287-4501, Tempe, AZ, USA*

oliver.niehuis@gmail.com

We are studying the genetics of hybrid-breakdown in the parasitoid wasp genus *Nasonia* by analyzing nuclear-cytoplasmic and nuclear-nuclear genic interactions in F_2 hybrid male populations. Under Mendelian inheritance, a 1:1 ratio of parental alleles is expected in hemizygote (haploid) F_2 hybrids. A significant deviation from this ratio (i. e., transmission ratio distortion or TRD) suggests either differential mortality of individuals bearing a particular genotype combination, or the release of a meiotic drive system in the F_1 hybrid generation. The generation of a linkage map allowed us to map the genomic regions, which harbor distorting loci. Our data indicate that dysfunctional nuclear-cytoplasmic interactions account for a significant proportion of the observed F_2 hybrid-breakdown in *Nasonia.* Since early embryos do not show a biased recovery rate of parental alleles, meiotic drive cannot explain the observed TRD in adult wasps. The mitochondrial electron transport system (ETS) consists of both nuclear and mitochondrial encoded proteins and, hence, is a promising candidate for explaining dysfunctional nuclear-cytoplasmic epistasis in hybrids. We identified the majority of ETS genes in the recently sequenced *Nasonia* genome. This enables us to analyze which of the genes map in the same genomic regions for which we identified distorting loci. To select promising candidates among the hundreds of ETS genes, we are currently assessing the efficiency of each ETS complex in hybrids by means of bio-essays.

16-05 Talk

DETECTING CYTONUCLEAR CONFLICTS BY COMPARING INTROGRESSION RATES BETWEEN MITOCHONDRIAL AND NUCLEAR DNA IN TWO ZONES OF SECONDARY CONTACT BETWEEN LARGE GULLS.

Laurene Gay [1], Pierre-Andre Crochet [2]

[1] *University of Exeter Cornwall, Centre for Ecology and Conservation, TR10 9EZ, Penryn, UK*
[2] *Centre d'Ecologie Fonctionnelle et Evolutive, 1919 route de Mende, 34293, Montpellier, France*

l.gay@exeter.ac.uk

Post-mating isolation can result from the breaking up of coadapted gene pools, in particular between mitochondrial and nuclear DNA. Incomplete reproductive isolation promotes gene flow between diverging taxa, but any gene involved in the reproductive barriers will be less prone to introgression than neutral markers. Consequently, if mtDNA contributes to post-mating isolation, then it would introgress at a slower rate compared to the neutral nuclear alleles.

We compared introgression patterns between fragments of mitochondrial genes and nuclear markers, neutral or under selection, in two zones of secondary contact between large gull species. If mitochondrial DNA is involved in the barrier to gene flow, we would expect restricted introgression compared to neutral markers and similar to the phenotypic traits under disruptive selection.

In the American hybrid zone, the cline in mitochondrial haplotypes did not differ significantly from the clines in nuclear allele frequencies in centre and slope. The introgression rate for phenotypic traits involved in reproductive isolation was lower compared to both nuclear and mitochondrial markers. However, in the European hybrid zone, cyto-nuclear linkage analyses detected asymmetric introgression of mitochondrial DNA and suggested that interspecific crosses may be more successful in one direction.

Only one of the two studied hybrid zones presented evidence for restricted introgression of mtDNA. This suggests that it more likely results from pre-mating barriers (asymmetric mate choice) rather than from the breaking up of cyto-nuclear coadaptations, because we expect similar postmating barriers between these closely related taxa.

16-06 Talk

MITOCHONDRIAL DNA HETEROPLASMY AND RECOMBINATION IN A REPTILIAN SECONDARY CONTACT ZONE.

Andreia F. Miraldo [1], Godfrey M. Hewitt [1], Octavio S. Paulo [2], Brent C. Emerson [1]

[1] *UEA, Biological Sciences, NR4 7TJ, Norwich, United Kingdom*
[2] *FCUL, Departamento de Biologia Animal, Lisboa, Portugal*

a.miraldo@uea.ac.uk

Inheritance of mitochondrial DNA in animals is thought to be both strictly maternal and non-recombining. Nevertheless, in the last decade evidence for recombination of mitochondrial DNA has been observed in several animal species, but few reports come from natural populations and most of the time the frequency of individuals possessing more than one mtDNA type is very low. Here we present direct evidence for extensive heteroplasmy and mitochondrial recombination in a region of secondary contact of a lizard species (*Lacerta lepida*). Individuals at the centre of the contact zone possess heteroplasmic point mutations at the mtDNA cytochrome b gene. The heteroplasmic condition was further tested by cloning 20 individuals at the centre of the zone and sequencing 8 to 10 clones per individual. All individuals tested had more than 4 types of recombinant mtDNA sequences as well as the parental types. The results suggest that mtDNA recombination was derived from the fusion of the maternal and paternal mtDNAs due to paternal leakage, which is thought to be more frequent in hybrid zones. The presence of several point mutations within recombinant sequences suggests that some recombination events are of some antiquity, but is ongoing and frequent within this species. To our knowledge this is the first study reporting such extensive heteroplasmy and recombination in the mtDNA genome in natural populations of a species with typical maternal mtDNA inheritance. Our findings suggest that mtDNA may recombine regularly and that secondary contact zones, where highly divergent molecules come into contact, may provide natural laboratories for studying this phenomenon.

16-07 Talk

CAN NEGATIVE CYTONUCLEAR INTERACTIONS EXPLAIN MTDNA PATTERNS IN BOMBINA HYBRID ZONES?

Jacek M. Szymura [1], Maciej Pabijan [1], Sebastian Hofman [1], Günter Gollmann [2], Anna Wandycz [1]

[1] *Jagiellonian University, Comparative Anatomy, Ingardena 6, 30-060, Kraków, Poland*
[2] *Universität Wien, Althanstraße 14, A-1040, Wien, Austria*

szym@zuk.iz.uj.edu.pl

Recently we analyzed pattern of mtDNA variation across several transects finding no evidence for free mtDNA movement, but at the same time only a weak cytonuclear disequilibria between mtDNA haplotypes and unlinked diagnostic allozymes. To back these studies we made a large phylogeographic survey of mtDNA variation in both species, again finding no evidence of mtDNA introgression between the species. mtDNA of *B.bombina* and *B.variegata* appear highly divergent and *K2P* distance of ~9% suggests pre-Pleistocene split of the species and an independent history. We have obtained complete sequences of mtDNA from distinct phylogeographic groups to infer patterns of non-synonymous substitutions and identified several non-conservative substitutions which may be targets for selection. Although direct evidence is lacking, large phenotypic, ecological and molecular divergence of these parapatric species make a strong argument for inferred negative epistatic effects underlying hybrid zone dynamics.

16-01 Poster

TRANSITION OF THE X CHROMOSOME ACROSS A MOUSE HYBRID ZONE IN CENTRAL EUROPE

Petra Dufkova [1], Pavel Munclinger [2], Milos Macholan [3], Barbora Bimova [1], Jaroslav Pialek [1]

[1] *Institute of Vertebrate Biology, Department of Population Biology, Studenec 122, Konesin, Czech Republic*
[2] *Charles University, Department of Zoology, Prague, Czech Republic*
[3] *Institute of Animal Physiology and Genetics, ASCR, Laboratory of Mammalian Evolutionary Genetics, Brno, Czech Republic*

dufkop@seznam.cz

There are numerous records in the evolutionary literature proposing that the X chromosome plays a significant role in reproductive isolation and hence in the processes of speciation. Reproductive barriers arise during mating between closely related but genetically different taxa. This work combines advantages of laboratory research and the existence of a natural zone of hybridization between two subspecies of the house mouse, *Mus musculus musculus* and *M. m. domesticus* in Europe. Mice were sampled from 1992 to 2006 in western Bohemia (Czech Republic) and northeast Bavaria (Germany). More than 2000 mice from 146 localities were scored for 11 X–linked molecular markers of known chromosomal position. These markers are based on insertion of DNA fragments into *musculus* or *domesticus* genome and extend from 16Mb to 158 Mb on the X chromosome. Introgression of each marker was evaluated using cline shape parameters (centre and width) calculated by the *ClineFit* programme. Comparisons of all estimated widths suggest two candidate regions for reproductive isolation in the proximal and central part of the X chromosome and might indicate possible regions associated with speciation.

Keywords: house mouse, hybrid zone, introgression, natural selection, reproductive isolation, speciation, X chromosome

16-02 Poster

CYTONUCLEAR ASSOCIATIONS IN BOMBINA HYBRID ZONES FROM THE DANUBE BASIN

Günter Gollmann [1], Sebastian Hofman [2], Maciej Pabijan [2], Jacek M. Szymura [2]

[1] *Univ. Vienna, Evolutionary Biology, Althanstr. 14, 1090, Vienna, Austria*
[2] *Jagiellonian University, Comparative Anatomy, Ingardena 6, 30-060, Kraków, Poland*

guenter.gollmann@univie.ac.at

The fire-bellied toads, *Bombina bombina* and *Bombina variegata*, are parapatrically distributed species which hybridize along their contact. Each species is composed of geographically differentiated groups. In central Europe, the lowlands along the Danube are occupied by the southern *B. bombina* group, which interacts with the Carpathian *B. variegata* along the southern slopes of the Carpathians, and with western *B. variegata* along the southern and western boundaries of the Danubian plains. Six transects across hybrid zones in Austria, Hungary and Slovakia were analysed for variation at five unlinked allozyme loci and mtDNA. Sampling across transect varied; central or marginal populations are lacking in particular transects. Southern *B. bombina* established contacts with the western *B. variegata* lineage in one transect, and with the Carpathian *B. variegata* lineage in the five others. Current distribution of *Bombina* is heavily affected by human activities. Population structures in the hybrid zones deviate somewhat from a clinal pattern; in some transects bimodal distributions of hybrid genotypes were found, in other transects a recent shift in hybrid zone position is likely. In all transects, mtDNA haplotypes and allozyme markers showed similar patterns of transition. Haplotypes of both species were found in the central sites, whereas marginal populations were mostly homogenous and contained haplotypes expected from toad morphology and allozymes.

16-03 Poster

CHLOROPLAST VARIATION IN EUROPEAN SILENE DIOICA AND S. LATIFOLIA: GEOGRAPHIC PATTERN AND HAPLOTYPE-SHARING

Louise A. Hathaway [1], Stefan Andersson [1], Honor C. Prentice [1]

[1] *Lund University, Plant Ecology and Systematics, Sölvegatan 37, 22362, Lund, Sweden*

louise.hathaway@ekol.lu.se

The dioecious herbs Silene dioica and S. latifolia are widespread throughout most of Europe. The species are closely-related, hybridize readily to produce fertile F1 hybrids, and may form hybrid swarms when they are brought into contact by anthropogenic disturbance. However, these hybrid swarms are short-lived in the absence of continued disturbance, and the species are naturally prevented from hybridizing by differences in habitat. Chloroplast polymerase chain reaction restriction-fragment length polymorphism (cpPCR-RFLP) markers were used to investigate patterns of postglacial migration and hybridization. Data from six markers were collected from 124 S. dioica populations and 74 S. latifolia populations from throughout Europe. Twenty-eight haplotypes were identified, four of which were widespread and 24 rare. The geographic structuring of the widespread haplotypes is similar to that seen in many European tree species. Three of the four widespread haplotypes were found in both species, and the geographic distribution of each haplotype was similar in both species. The distributions of the three widespread, shared haplotypes suggest that they were restricted to different refugial regions in S Europe/the Mediterranean during the last ice-age, and the sharing of these haplotypes in S. dioica and S. latifolia is most plausibly explained by historical hybridization. The fourth common haplotype was restricted to Fennoscandian populations of S. dioica. We suggest that this haplotype may have been found in NE refugia containing only S. dioica during the last ice-age and migrated south through Fennoscandia during the post glacial period. Only seven of the rare haplotypes were found in more than one population and, despite extensive overlap in the distribution of the common haplotypes, 80% of the populations only contained one haplotype. Only four of the rare haplotypes were found in both species.

16-04 Poster

HALDANE'S RULE IN HAPLODIPLOIDS: THE UNDERESTIMATED EFFECT OF CYTONUCLEAR INCOMPATIBILITIES

Tosca Koevoets [1], Louis P. W. G. M. Van de Zande [1], Leo W. Beukeboom [1]

[1] *University of Groningen, Evolutionary Genetics, Kerklaan 30, 9751 NN, Haren, The Netherlands*

t.koevoets@rug.nl

Crosses between two haplodiploid parasitic wasps *Nasonia vitripennis* and *N. giraulti* showed that F_1 hybrid females did not suffer from hybrid incompatibilities, while their F_2 male offspring showed an increased level of mortality compared to pure strain F_2 males. This trend in hybrid incompatibilities is reminiscent of a rule described by Haldane, that states that "when in the offspring of two different animal races one sex is absent, rare or sterile, that sex is the heterozygous [heterogametic] sex". However, the problem with Haldane's rule and haplodiploidy is that technically it does not apply since sex chromosomes are lacking in haplodiploids. Thus the question is raised *why* haplodiploids seem to follow Haldane's rule and whether the genetic basis in haplodiploids is the same for diploids *with* sex chromosomes.

We investigated the hybridization of *N. vitripennis* and *N. longicornis*. Hybrids in one direction of the cross did not suffer from hybrid incompatibilities, while the reciprocal cross showed dramatic mortality and sterility of the hybrid males. These results point at cytonuclear incompatibilities as the cause of hybrid breakdown in *Nasonia*. Using a genome-wide screen with microsatellite markers, loci are identified that show a drop-out in hybrid adult males (as compared to hybrid embryo males). The final goal of the study is to identify the genes that are responsible for cytonuclear incompatibilities in these hybrids.

16-05 Poster

EVIDENCE FOR HYBRIDISATION AND INTROGRESSION AMONG ABIES MILL. SPECIES IN EUROPE

Sascha Liepelt [1], Eike Mayland-Quellhorst [1], Birgit Ziegenhagen [1]

[1] *Philipps-Universität Marburg, Conservation Biology, Karl-von-Frisch-Str., 35032, Marburg, Germany*

liepelt@staff.uni-marburg.de

The European *Abies* species complex has been a constant puzzle for taxonomists. Previous studies have tried to shed light on the relationships among species, subspecies and so called hybrid species. Reproductive barriers among species on the same continent appear to be weak, while hybridisation across continents seems impossible in experimental crosses. But does this mean, that European species hybridize regularly or did so in the past?

Chloroplast and mitochondrial DNA exhibit contrasting modes of uniparental inheritance in this genus which offers the chance to take a closer look into the mechanisms of hybridisation. We applied molecular markers from both organelles to determine the extent of hybridisation and introgression among European fir species.

The results from mtDNA contrasted sharply with the results from cpDNA. The mtDNA markers allowed us to differentiate among maternal lineages, whose geographic distribution is bound to dispersal by seeds. These maternal lineages were sharply separated among species or groups of species and exhibited almost no introgression.

A completely different picture was observed with cpDNA markers where the variants are distributed first by pollen and then by seeds, due to paternal inheritance. Paternal lineages were not restricted to single species and the Central European *Abies alba* Mill. contained all of the observed cpDNA variants and paternal lineages, respectively. Allele frequency clines even suggested postglacial gene flow among parapatric species.

The existence of a common gene pool for the European fir species will be discussed for evolutionary implications.

16-06 Poster

MOLECULAR PHYLOGEOGRAPHY OF TWO SIBLING SPECIES OF EUREMA BUTTERFLIES AFFECTED BY WOLBACHIA INFECTION SWEEP

Satoko Narita [1], Masashi Nomura [1], Yoshiomi Kato [2], Takema Fukatsu [3]

[1] *Chiba University, Faculty of Horticulture, 648, 271-8510, Matsudo, Chiba, Japan*
[2] *International Christian University, Dept. Biology, 181-8585, Tokyo, Japan*
[3] *AIST, Inst. Biol. Res. Func., 305-8566, Tsukuba, Ibaraki, Japan*

narita3105@graduate.chiba-u.jp

It was recently recognized that in Japan, the common yellow butterfly, Eurema hecabe, consists of two sibling species, which have been unnamed yet and tentatively called yellow (Y) type and brown (B) type. We investigated the diversity of nuclear and mitochondrial genes, *ND5* and *16SrDNA*, in Japanese populations of Y type and B type of *E. hecabe*. The phylogeny based on nuclear genes, *EF1-α* and *Tpi*, agreed with the distinction between Y type and B type, which had been also supported by a wide array of biological data. However, the phylogeny based on mitochondrial genes did not reflect the distinction. PCR survey of *Wolbachia* revealed that B-type populations were all infected while Y-type populations contained both infected and uninfected individuals. A single genotype of *Wolbachia*, which was inferred to be a CI-inducing strain from their *wsp* gene sequence, was prevalent in these populations. Notably, the mitochondrial phylogeny was in perfect agreement with the pattern of *Wolbachia* infection, suggesting that the *Wolbachia* infection had affected the mitochondrial genetic structure of the host insects. On the basis of these results together with the geological and biogeographical knowledge of the Japanese Archipelago, we proposed an evolutionary hypothesis on the invasion and spread of *Wolbachia* infection in B-type and Y-type of *E. hecabe*.

16-07 Poster

THE BALTIC SEA HYBRID ZONE BETWEEN PACIFIC AND ATLANTIC LINEAGES OF MACOMA BALTHICA

Raisa Nikula [1, 2], Petr Strelkov [3], Risto Väinölä [2]

[1] *University of Helsinki, Department of Environmental and Biological Sciences, Helsinki, Finland*
[2] *Finnish Museum of Natural History, Helsinki, Finland*
[3] *St. Petersburg State University, Department of Ichtyology and Hydrobiology, St. Petersburg, Russia*

raisa.nikula@helsinki.fi

A postglacial contact of Pacific and Atlantic lineages of the marine bivalve Macoma balthica has taken place in the marginal Baltic Sea basin. The independent evolution of the lineages dates back to at least 2 million years, and introgressive hybridization between them in the Baltic Sea has likely been going on for nearly 10 000 years. We examined the geographic clines and genotypic structure of the Baltic Macoma in 10 nuclear allozyme loci and mitochondrial DNA across a 1000 km wide transect from the marine North Sea to the oligohaline Northern Baltic. From nuclear genotypic structure, the inner Baltic populations appear as an equilibrium hybrid swarm of Pacific and Atlantic lineages in 60%:40% proportions, whereas they are almost fixed for the Pacific mitochondrion. The genetic transition zone between this swarm and the Atlantic taxon, in the Western Baltic – Kattegat, is wide but does not follow a simple monotonous geographical pattern. The clines in mtDNA and in different nuclear characters also differ significantly in their location and width. The degrees of introgression are different along the southern/eastern and the western coasts of the Baltic, and different in the nearshore and deeper bottoms, broadly in agreement with the general patterns of circulation and salinity stratification in the area. Relatively strong inter-locus genotypic associations and cytonuclear associations were found in places in the transition zone. Inter-locus nuclear associations were maximally half of those expected in a situation where no interbreeding between the inner Baltic and and North Sea stocks would take place; the relative cytonuclear associations seemed on average weaker than those between nuclear loci.

16-08 Poster

SEX-BIASED GENE FLOW BETWEEN HOST-STRAINS IN THE FALL ARMYWORM, SPODOPTERA FRUGIPERDA

Gerhard Schöfl [1], David G. Heckel [1]

[1] *Max-Planck Institute for Chemical Ecology, Entomology, Hans-Knöll Straße 8, 07745, Jena, Germany*

gschoefl@ice.mpg.de

The noctuid moth *Spodoptera frugiperda* may be diverging into two genetically differentiated, broadly sympatric strains associated with different larval host plants, namely corn and rice. These strains are morphologically indistinguishable and reliable identification can only be achieved by mitochondrial haplotyping (Nagoshi et al. 2006). Gene flow between the strains is thought to be minimized by premating isolation mainly based on temporal differences, i.e. the corn strain mates early in the night while the rice strain mates late during night (Pashley et al. 1992) We have estimated genetic differentiation using nuclear (AFLPs) and mitochondrial (COI and 16S-ND1 haplotypes) markers in corn and rice populations. Levels of differentiation among populations at nuclear markers are lower than the level of differentiation at mitochondrial markers. Only the differentiation at the latter is concordant with strain boundaries. These data suggest that female-mediated gene flow between strains is reduced compared to male-mediated gene flow. Laboratory crosses between the two strains in both directions (C♀×R♂and R♀×C♂) result in fertile F1-progeny at a rate similar to within-strain crosses. The offspring of C♀×R♂ crosses is significantly male-biased (35% fewer females than males), indicating some degree of postzygotic isolation between strains. Crossing (R♀×C♂)-hybrid females to males of either parental strain mostly fails, while all other backcross combinations yield fertile clutches. Thus, the restricted female-mediated gene flow across strain boundaries is probably due to: a) behavioural asymmetries between the sexes and b) stronger counterselection of female hybrids in accordance with Haldane's rule for ZW species. The extensive similarity of the nuclear genome between strains suggests that selection on a limited number of characters is important in maintaining the differences between these strains and that the number of loci involved in this process is quite low.

16-09 Poster

VARIATION IN INTROGRESSION DUE TO RARE HYBRIDISATION IN A HYBRID ZONE BETWEEN RED AND SIKA DEER (GENUS CERVUS): INVESTIGATING THE INFLUENCE OF STOCHASTICITY

Helen V. Senn [1], Nick H. Barton [1]

[1] *University of Edinburgh, Institute of Evolutionary Biology, West Mains Road, EH9 3JT, Edinburgh, UK*

h.v.senn@sms.ed.ac.uk

If a hybrid zone is surveyed with a panel of diagnostic molecular markers, chance will play a large role in the formation of their pattern of introgression if hybridisation is rare. Rare hybridisation can be approximated as a successive chain of backcrosses into one or other of the parental populations, with the expected proportion of introgressing alleles decreasing by one half every generation. Stochastic events associated with the initial generations of backcrossing have a large effect on the pattern of introgression in subsequent generations. In contrast, say, to the Eastern European *Bombina bombina* x *B. variegata* hybrid zone, the hybrid zone between native *Cervus elaphus* and invasive *C. nippon* in Argyll, Scotland, is an example where hybridisation is rare (1:500 to 1:1000 matings). Despite this, introgression is extensive (~40%). We use a stochastic model of gene flow via backcrossing to understand the potential effect of chance on the pattern of introgression in this hybrid zone. This enables us to understand the limits of our ability to detect other factors that may influence the pattern of introgression, such as selection and asymmetric mating, in this and similar scenarios.

16-10 Poster

EVIDENCE OF NATURAL HYBRID TAXON IN SALMONIDS: CAPTURE OF BROWN TROUT MTDNA THE JADRO SOFTMOUTH TROUT

Aleš Snoj [1], Steven Weiss [2], Tea Tomljanović [3], Bo Delling [4], Tomislav Treer [3], Simona Sušnik [1]

[1] *University of Ljubljana, Biotechnical Faculty, Department of Animal Science, Groblje 3, SI 1230, Domzale, Slovenia*
[2] *Karl-Franzens Universität Graz, Institut für Zoologie, Universitätsplatz 2, A 8010, Graz, Austria*
[3] *University of Zagreb, Faculty of Agriculture, Department of Fisheries, Svetošimunska 25, 1000, Zagreb, Croatia*
[4] *Swedish Museum of Natural History, Department of Vertebrate Zoology, POB 50007, S-104 05, Stockholm, Sweden*

ales.snoj@bfro.uni-lj.si

Softmouth trout (*Salmo obtusirostris*) occur in restricted area of five rivers (Krka, Jadro, Vrlika, Neretva and Zeta) of the Adriatic basin in the SW Balkans. While molecular phylogeny and taxonomic status of the Neretva softmouth trout was recently established, question concerning the evolutionary origin of the Jadro softmouth has remained. In order to answer this question, Neretva softmouth trout and Jadro softmouth trout along with two neighbouring populations of brown trout (*Salmo trutta*) were analysed with mtDNA and nuclear genes, and nine microsatellites. The Jadro softmouth were fixed for a brown trout mtDNA haplotype of the Adriatic lineage, which is 1.7% divergent from a previously described haplotype characteristic for the Neretva softmouth. All other genetic markers, as well as morphological analysis, supported the clear distinction of softmouth trout from the rivers Neretva and Jadro from brown trout in neighbouring populations, and thus a mtDNA capture event is assumed. Population specific microsatellite allele profiles, as well as a high number of private alleles for both populations of softmouth trout, support the hybridization between brown trout and the Jadro softmouth trout most likely being of ancient origin. This mechanism generating a reticulate evolutionary pathway demonstrates how mtDNA can provide patterns of genetic differentiation very different from that obtained with nuclear genes and can lead to inaccurate conclusions between populations in absence of any other genetic data.

16-11 Poster

HYBRIDIZATION IN CALOPTERYX DAMSELFLIES: THE ROLE OF MALE ALTERNATIVE MATING TACTICS

Kaisa J. Raatikainen [1], Katja Tynkkynen [1], Elina Haukilehto [1], Matti Häkkilä [1], Janne S. Kotiaho [1]

[1] *University of Jyväskylä, Dept. of Biological and Environmental Science*

katynkky@bytl.jyu.fi

Hybridization between two closely related species may occur because of problems in species recognition or because of adaptive mating decision. In the latter, an individual does better by reproducing with heterospecific than not breed at all. However, this happens only if at least some fertile hybrid progeny is produced. In species in which alternative male mating tactics (e.g. territorial and non-territorial tactics) exist, it could be that males with reproductively inferior tactics are not so choosy and thus may mate also with heterospecifics. In this study, we investigated whether male readiness to mate with heterospecific females is dependent on male tactic in the damselfly, *Calopteryx splendens*. In this species, it has been previously showed that males have poor premating reproductive isolation, and males frequently court females of related species, *C. virgo*. We tested male readiness to mate with heterospecifc females by presenting females to males with different reproductive tactics, and by recording the courting activity of males. In contrast to our prediction, males with non-territorial tactics were not as ready to mate with *C. virgo* as territorial *C. splendens* males. Actually, males which were most eager to mate with heterospecifics were territorial males with large wing spots indicating their high quality. The result can be explained if high quality, territorial males have most optimal cost: benefit-ratio for the behaviour. There are costs if a male mistakenly court and mate with heterospecific females. However, the high courting activity may benefit the male if it means that he does not miss conspecific females as often as less courting males.

16-12 Poster

INTERSPECIFIC ASYMMETRY OF MATING PREFERENCES AND HYBRID FITNESS IN CHORTHIPPUS GRASSHOPPER SPECIES HYBRIDIZING IN UKRAINE

Varvara Y. u. Vedenina [1]

[1] *Institute for Information Transmission Problems, Russian Academy of Sciences, Bolshoi Karetnyi per. 19, 127994, Moscow, Russia*

vedenin@iitp.ru

Two closely related grasshopper species *Chorthippus albomarginatus* (CA) and *Ch. oschei* (CO) were shown to form a mosaic bimodal hybrid zone stretching over a distance of 200 km on the territory of Ukraine and Moldova. The species are similar in morphology and the calling songs, but different in their courtship songs. The song of CA that is supposed to be a more ancient species consist of three different elements, whereas the song of CO possesses five elements and is accompanied by a characteristic visual display. We studied premating and postmating isolating barriers between the hybridizing species. In choice mating experiments, the females of both species demonstrated a strong assortative mating. However, when the females were allowed to choose between conspecific and hybrid males, an asymmetry in mating preference was observed. The CO females preferred conspecific males to hybrid males, whereas the CA females did not distinguish between conspecific and hybrid males. The hybrid F_1 females, irrespective of the direction of cross, behaved as the CA females. Asymmetry in mating preference can be due to the unusual inheritance pattern of the courtship song we found in these species. Comparison of the parental and hybrid viability revealed a reduced hatching and increased larval mortality in F_1 and F_2 hybrid generations, however, hybrid unfitness was stronger in one direction of cross when CO had been used as a maternal species. Thus, we indicate a correlation of asymmetry in mating preference with hybrid viability. We suggest stronger introgression from CO (derived species) to CA (ancestral species) than vice versa, which is supported by the song analysis from the same hybrid localities conducted in different years.

16-13 Poster

COMPARING AND COMBINING GENOME-WIDELY DEVELOPED SINGLE NUCLEOTIDE MARKERS AND MICROSATELLITES FOR IDENTIFICATION OF HYBRIDS BETWEEN GREATER AND LESSER SPOTTED EAGLES

Ülo Väli [1], Hans Ellegren [1]

[1] *Uppsala University, Department of Evolutionary Biology, Norbyvägen 18D, SE-75236, Uppsala, Sweden*

ulo.vali@ebc.uu.se

Genetic identification of hybrid individuals is important in hybridisation studies but choosing the appropriate set of markers may be complicated, and allopatric reference samples of rare species are sometimes hard to collect. In current study we demonstrate the development of single nucleotide polymorphic markers (SNPs) for detection of hybrids between threatened Greater and Lesser Spotted Eagles using individuals from a sympatric population, and compare the efficiency of SNPs with this of microsatellites. We amplified introns from 122 avian genes, obtained single-band PCR products from 87 introns, and sequenced 48 of them in eleven spotted eagles. Using Bayesian model-based approach, nine SNPs (eight of them detectable by restriction analysis) were finally selected and tested successfully in 65 sympatric and allopatric spotted eagles, and their hybrids. Comparatively, only one out of twelve previously described avian nuclear intron markers showed significant species-specific allelic difference. Twenty microsatellites outperformed nine SNPs in species identification, but were poorer in hybrid detection, whereas power of ten microsatellites remained too low for correct assignment. Combined use of nine SNPs and twenty microsatellites resulted to most efficient and accurate identification of all individuals.

16-14 Poster

THE PHYLOGEOGRAPHY OF THE CRESTED NEWT TRITURUS KARELINII FROM THE EASTERN MEDITERRANEAN BASIN: DISTINCT MITOCHONDRIAL HAPLOTYPES OCCURRING SYNTOPIC

B. Wielstra [1], J. W. Arntzen [1], G. Themudo [1]

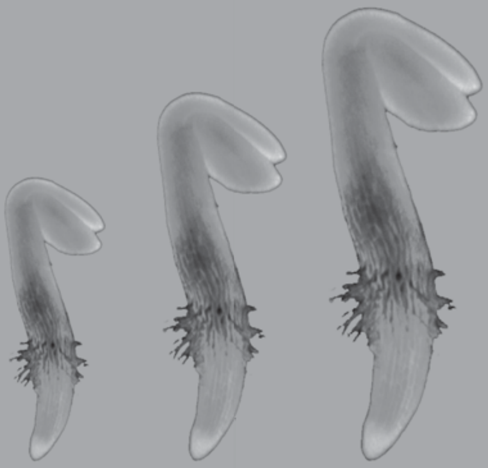
[1] *National Museum of Natural History, P.O. Box 9517, 2300 RA, Leiden, The Netherlands*

wielstra@hotmail.com

The *Triturus cristatus* superspecies – the crested newts – is a group of closely related, mostly parapatric salamander taxa, inhabiting the Western Palaearctic. Intraspecific variation is low in the European part of the crested newt distribution, on which previous research has focussed. *T. karelinii* occurs in the Eastern Mediterranean Basin: a region which, although it promises to hold interesting biogeographical patterns due to its turbulent geological history, is relatively understudied from a phylogeographical point of view. By using a dense geographical sampling strategy, sequence data from a variable mitochondrial marker (the ND4 gene), and a Bayesian phylogenetic analysis, this study uncovers the genetic structuring within *T. karelinii*. Three phylogroups are present and monophyly of the taxon is rejected. The allopatric population from Caucasia comprises a homogenous phylogroup, not closely related to the others. The *T. karelinii* cluster from Northern Turkey and the one from Western Turkey and the Balkans are both subjected to strong substructuring. A sister relationship between both these phylogroups is found and representatives from each occur syntopic along the Sakarya river in the north-west of Turkey. Furthermore, a ring-like structure is present in the phylogroup from Western Turkey and the Balkans: two distinct haplotypes, connected by intermediate ones occurring along the Sea of Marmara, meet in Trace (European Turkey).

Why MHC makes the difference – its role in various fields

17



Saturday August 25 *Location*: Ekonomikum 4

Symposium 17: Why MHC makes the difference – its role in various fields

ORGANIZERS: Tobias Lenz, Max Planck Institute for Evolutionary Biology, Germany
Christophe Eizaguirre, Max Planck Institute for Evolutionary Biology, Germany

9.45-10.15	**Simone Sommer** (invited) Genes, health & sex: the role of immune gene variability (MHC) in parasite resistance and mate choice
10.15-10.45	**Gabriele Sorci** (invited) Adaptive MHC variation in a non-model species
10.45-11.05	**Karin Berggren** Allelic combinations of promoter and exon 2 in DQB1 in dogs and wolves.
11.05-11.35	*Coffee*
11.35-11.55	**Mark Gillingham** MHC and sexual selection in the fowl, Gallus gallus
11.55-12.15	**Nina Schwensow** MHC, parasites and mate choice in a free living primate
12.15-12.35	**Claire Loiseau** Antagonistic effects of a MHC Class I allele on malaria infected house sparrows
12.35-12.55	**Dustin Penn** MHC genes and individual odour
12.55-14.00	*Lunch*

17-01 Talk

GENES, HEALTH & SEX: THE ROLE OF IMMUNE GENE VARIABILITY (MHC) IN PARASITE RESISTANCE AND MATE CHOICE

Simone Sommer [1]

[1] *Leibniz-Institute for Zoo- and Wildlife Research, Evolutionary Genetics, Alfred-Kowalke-Str. 17, 10315, Berlin*

sommer@izw-berlin.de

Current discussions in evolutionary ecology and conservation genetics focus on the relative importance of using selective neutral markers or markers of coding genes to identify adaptive and evolutionary relevant processes. In vertebrates, growing evidence suggests that genetic diversity is particularly important at the level of the major histocompatibility complex (MHC) because its gene products play an important role in immune functions. Moreover, MHC genes are considered as one of the best candidates for the genetic basis of mate choice in vertebrates. According to current hypotheses genetic benefits can be obtained if the risk of genetic incompatibility between maternal and paternal genomes is minimised by avoiding mating with close kin (inbreeding avoidance), or by increasing the genetic heterozygosity or diversity within the progeny. Females might also choose males with different MHC-alleles as mating partners to increase the genetic variability of offspring and thus their resistance to infectious diseases. We investigated the importance of MHC genes in gastrointestinal parasite resistance and female mate choice in free-ranging mammals which differed in their mating systems (monogamous – promiscuous) by analyzing overall genetic variability as well as a MHC-marker of adaptive significance. The possible genetic benefits of female preferences on fitness parameters such as parasite resistance as well as the role of different life history strategies are discussed.

17-02 Talk

ADAPTIVE MHC VARIATION IN A NON-MODEL SPECIES

Gabriele Sorci [1]

[1] *CNRS, Biogeosciences, 6 Boulevard Gabriel, 21000, Dijon, France*

gabriele.sorci@u-bourgogne.fr

How MHC variation is maintained is still a matter of discussion, especially in natural populations of non-model species. Empirical evidence suggesting that pathogens contribute to the maintenance of MHC variation mostly comes from studies on lab mice. In the last years, we have been studying the interaction between MHC polymorphism and avian malaria in the house sparrow. Using both epidemiological surveys and experimental infections, we explored the potential for avian malaria to result in adaptive MHC diversity. In particular, we suggest that interactions between hosts and parasites may result in a pattern of local adaptation, with different MHC alleles positively selected by local strains of Plasmodium and Haemoproteus species.

17-03 Talk

ALLELIC COMBINATIONS OF PROMOTER AND EXON 2 IN DQB1 IN DOGS AND WOLVES

Karin T. Berggren [1], Jennifer M. Seddon [2]

[1] *Uppsala university, Evolutionary biology, Norbyvägen 18D, 75236, Uppsala, Sweden*
[2] *University of Queensland, School of Veterinary Science, QLD 4072, St Lucia, Australia*

Karin.Berggren@ebc.uu.se

Major Histocompatibility Complex (MHC) gene polymorphism has been well documented in dogs. We extended these studies to include mapping of polymorphism in the proximal promoter regions of MHC genes in dogs and wolves. The results show high levels of polymorphism in the *DQB* promoter region. Polymorphism in promoter regions of humans and mice is known to affect expression of MHC genes. It is reasonable that the same is true in dogs and wolves.

We show haplotypic associations between particular *DQB1* exon 2 alleles and promoter variants, implying strong linkage disequilibrium in this region. It has also been suggested that co-selection between the promoter and the exon 2 region occurs as a result of selectively favourable promoter/exon 2 combinations, further enhancing the observed haplotypic patterns. Both wolves and dogs have significantly fewer promoter/exon 2 combinations than we would expect at random. Interestingly, we notice weaker haplotypic associations in dogs than in wolves. Dogs have twice as many promoter/exon 2 combinations as wolves and an almost 2-fold difference in the number of exon 2 alleles per promoter variant. Although fewer allelic combinations are expected than at random due to genetic linkage, the degree of reduction differs. Bottlenecks in wolf populations are a likely explanation for their increased linkage disequilibrium but, although similar population effects can be expected within a dog breed, this pattern differs with tested German Shepherd dogs. Weaker haplotypic association patterns in dogs could be explained by an increased rate of recombination in dogs or altered selection pressure, possibly as a result of the domestication process. Deviations from normal MHC expression patterns have been associated with autoimmune diseases, which occur frequently in several dog breeds. Further knowledge about these deviations may help us understand the source of such diseases.

17-04 Talk

MHC AND SEXUAL SELECTION IN THE FOWL, GALLUS GALLUS

Mark A. F. Gillingham [1], Charlie K. Cornwallis [1], Kirsty Worley [2], Hanne Løvlie [3], Jim Kaufman [4], David Richardson [2], Tommaso Pizzari [1]

[1] *The University of Oxford, Zoology, Tinbergen Building, South Parks Road, OX1 3PS, Oxford, England*
[2] *The University of East Anglia, School of Biological Sciences, The University of East Anglia, NR4 7TJ, Norwich, England*
[3] *Stockholm University, Department of Zoology, Stockholm University, 106 91, Stockholm, Sweden*
[4] *Institute for Animal Health, Institute for Animal Health, Institute for Animal Health, RG20 7NN, Compton, England*

mark.gillingham@zoo.ox.ac.uk

The major histocompatibility complex (MHC) genes are highly polymorphic and code for antigen presenting molecules which have an important immunological role in the recognition of self and non-self. MHC heterozygotes may be able to resist a wider range of pathogens. Selecting a partner according to MHC compatibility may thus increase offspring fitness through: (1) improved pathogen resistance, and (2) inbreeding avoidance. However, the role of the MHC in partner choice and other mechanisms of sexual selection remains poorly understood. Here, I present novel results on MHC-mediated mechanisms of pre- and post-insemination sexual selection in the red junglefowl, Gallus gallus, a bird which is characterised by intense sexual selection and a simple structure of the MHC.

17-05 Talk

MHC, PARASITES AND MATE CHOICE IN A FREE LIVING PRIMATE

Nina I. Schwensow [1], Joanna Fietz [2], Kathrin H. Dausmann [3], Simone Sommer [1]

[1] Leibniz-Institute for Zoo- and Wildlife Research (IZW), Evolutionary Genetics, Alfred-Kowalke-Str. 17, 10315, Berlin, Germany
[2] University of Ulm, Experimental Ecology, Albert-Einstein-Allee, 89081, Ulm, Germany
[3] University of Hamburg, Animal Ecology and Conservation, Martin-Luther-King-Platz 3, 20146, Hamburg, Germany

Schwensow@izw-berlin.de

We investigated the effects of neutral (microsatellite) versus adaptive genetic (MHC-DRB) variation in parasite resistance and mate choice in a natural population of fat-tailed dwarf lemurs (*Cheirogaleus* medius). The fat-tailed dwarf lemur is an obligate pair-living primate which maintains life-long pair bonds but has an extremely high rate of extra-pair paternity. Both mechanisms -mate choice and parasite driven selection- has been discussed as possible forces driving MHC variability. As in human medical studies, MHC-alleles were grouped into MHC-supertypes based on similarities in their functional important antigen binding sites. We found evidence for specific MHC-supertypes that were linked to susceptibility and resistance, respectively. The study further indicated that females preferred males both as social and as genetic fathers for their offspring having a higher number of MHC-alleles and MHC-supertypes, a lower overlap with female's MHC-supertypes as well as a higher genome wide heterozygosity than randomly assigned males. Mutual relatedness had no influence on mate choice. Females engaged in extra-pair mating shared a significant higher number of MHC-supertypes with their social partner than faithful females. Thus, our results indicate that MHC variability is influenced by both parasite-driven selection and mate choice.

17-06 Talk

ANTAGONISTIC EFFECTS OF A MHC CLASS I ALLELE ON MALARIA INFECTED HOUSE SPARROWS

Claire Loiseau [1], Rima Zoorob [2], Stephane Garnier [3], Julien Birard [4], Pierre Federici [1], Romain Julliard [4], Gabriele Sorci [3]

[1] Université Pierre et Marie Curie Paris VI, Parasitologie Evolutive, 7 quai St Bernard, 75005, Paris, France
[2] CNRS, Génétique Moléculaire, 7 rue Guy Mocquet, 94800, Villejuif, France
[3] Université de Bourgogne, Ecologie Evolutive, 6 bd Gabriel, 21000, Dijon, France
[4] Museum National d'Histoires Naturelles, Conservation des especes, 55 rue buffon, 75005, Paris, France

cloiseau@snv.jussieu.fr

Genes of the Major Histocompatibility Complex (MHC) play a fundamental role during the immune response since MHC molecules present antigenic peptides derived from invading pathogens to T-cells. In agreement with this prominent role, *Mhc* genes have been reported to be associated with decreased risk of contracting infectious diseases in humans, animal models and wildlife. Surprisingly, however, there is an almost equivalent number of studies that have reported associations between the presence of certain *Mhc* alleles and an accrued risk of being infected. From an evolutionary perspective, the existence of these susceptibility alleles is puzzling, since the cost generated by the infection should eliminate them from the population. We show that susceptibility alleles may be maintained in a population of house sparrows if they have antagonistic effects on different malaria species. We found that one *Mhc* class I allele was associated with an increased risk to be infected with a *Plasmodium* strain (SGS1), but with a reduction in the likelihood to harbour a *Haemoproteus* strain (PADOM3). We show that this antagonistic effect can account for the persistence of the susceptibility allele, if the fitness cost of the infection with PADOM3 is, at least, twice the cost induced by SGS1. We also provide an explanation for the emergence of this antagonistic effect based on the idea that pathogens sharing the same resources are involved in competition to establish within the host. Accordingly, the allele that confers resistance to PADOM3 may alter the outcome of the competitive interactions between PADOM3 and SGS1 and, as such, enhance the pool of hosts susceptible to SGS1 infection.

17-07 Talk

MHC GENES AND INDIVIDUAL ODOR

Dustin J. Penn [1], Elisabeth Oberzaucher [2], Karl Grammer [2], Gottfried Fischer [2], Helena Soini [2], Donald Wiesler [2], Milos Novotny [2], Sarah Dixon [2], Yun Xu [2], Richard Brereton [2]

[1] *Austrian Academy of Sciences, Konrad Lorenz Institute for Ethology, Savoyenstrasse 1a, 1160, Vienna, Austria*
[2]

D.Penn@klivv.oeaw.ac.at

The polymorphisms of the genes of the major histocompatibility complex (MHC) are maintained by balancing selection from pathogens, mating preferences, or both; however, the later hypothesis remains controversial. The main challenge for the mating preference hypothesis is to explain how MHC genes influence individual odor, and one possibility is that these genes shape individual microbiota. Our goals were to identify the volatile compounds comprising individual odor signatures in humans, and determine whether MHC genes or microbiota influence these compounds. We systematically collected axillary sweat and microbial samples from 196 subjects from 16 families living in a small village in the Austrian Alps. We performed chemical analyses of sweat (GC-MS chromatographic profiling) and genetic profiling (PCR-DGGE) of the microbial samples, and statistically analyzed the data using multivariate pattern recognition techniques. Our results support the idea that individuals have distinctive odor signatures and also microbiota, and we identified candidate compounds influenced by MHC genes.

17-01 Poster

MHC CLASS I AND RESISTANCE TO VIRAL AND PROTOZOAN INFECTIONS IN SCARLET ROSEFINCHES CARPODACUS ERYTHRINUS

Jan Schnitzer [1], Marta Promerova [2], Michal Vinkler [1], Pavel Munclinger [1], Jan Votypka [3], Josef Bryja [2], Tomas Albrecht [2]

[1] *Charles University in Prague, Department of Zoology, Vinicna 7, CZ-12844, Prague, Czech Republic*
[2] *Institute of Vertebrate Biology ASCR, v.v.i., Department of Population Biology, Studenec 122, CZ-67502, Studenec-Konesin, Czech Republic*
[3] *Charles University in Prague, Department of Parasitology, Vinicna 7, CZ-12844, Prague, Czech Republic*

albrecht@ivb.cz

Parasites represent one of the most important factors directing the animal evolution. As the host's body is exposed to virtually unlimited number of antigens originating from various potentially pathogenic particles a great pressure is posed on the diversification of many molecular components involved in immunity. This is especially true for binding sites of antigen recognition receptors. One of the most important gene clusters with such a function is the Major Histocompatibility Complex (MHC) which encodes molecules presenting peptide fragments of antigens to the T cells. This signal enables the development of adaptive immune response against intruding parasites. Since MHC class I is involved especially in the defence against intracellular parasites, we tested the hypothesis that allelic variability at MHC class I determine the occurrence of non-lethal viral infection caused by Avipox viruses and avian malaria caused by protozoan *Haemoproteus* in Scarlet Rosefinches. According to the predictions the number of MHC class I alleles was a good predictor of infestation with avian pox disease in the study population of rosefinches ($p<0.01$). On the other hand, there was no relationship between the MHC class I allelic diversity and *Haemoproteus* infestation. These data indicate that MHC class I could be involved in defence against viral diseases in rosefinches, but other mechanisms take place in the defence against protozoans inhabiting erythrocytes.

17-02 Poster

MAJOR HISTOCOMPATIBILITY COMPLEX AND SEXUAL ORNAMENTS IN THE COMMON PHEASANT

Mariella Baratti [1], Martina Ammannati [2], Alessandro Massolo [3], Francesco Dessì-Fulgheri [2]

[1] *C.N.R., Institute of Ecosystem Study, Via Madonna del Piano, 10, 50019, Sesto Fiorentino (FI), Italy*
[2] *University of Florence, Department of Animal Biology and Genetics, Via Romana, 17, 50125, Firenze, Italy*
[3] *University of Pavia, Department of Ainmal Biology, Piazza Botta, 9, 27100, Pavia, Italy*

hozomoon@tin.it

The ring-necked pheasant (*Phasianus colchicus*) is a species not endemic to Italy, but it is nevertheless an important species for Italian wildlife management. The common pheasant is polygamous and males are characterized by secondary sexual traits. Typical pheasant's male ornaments are the wattle, the tarsal spur and the tail, while the wattle seems to be the only secondary sexual character linked to the plasmatic levels of testosterone. The size of the wattle correlates with high testosterone level. According to the "good genes" hypothesis, choosy females can improve the genetic quality of their offspring by mating only with males that will contribute good genes to their offspring. Male ornaments function as good quality signals, inheritable from the progeny, appearing to be correlated with male viability and resistance to parasites. Only individuals with enhanced genetic resistance to parasites would be able to express better secondary sexual ornaments. We have explored the relationships between molecular variation and the wattle, analysing MHC polymorphism in natural and captive bred populations of the ring-necked pheasant. In particular we have analysed a captive-bred stock (n=70) and two natural populations (n=56) inhabiting protected areas in Tuscany. Genetic analyses have been carried out using amplifications, CE-SSCP, cloning and sequencing of a section of exon 2 of MHC gene, class IIB. This molecular analysis allowed us to describe 8 new PhcoMhc alleles. We studied the correlations between ornaments (wattle and tarsal spur) and MHC and we found an association between genetic polymorphism at PhCoMhc level and wattle size, suggesting that this trait may be, for the female, an honest signal of genetic quality.

17-03 Poster

MAJOR HISTOCOMPATIBILITY COMPLEX (MHC II) VARIATION IN THE GREAT CRESTED NEWT (TRITURUS CRISTATUS) SHOWS THE SOUTHERN RICHNESS – NORTHERN PURITY PATTERN

Wieslaw Babik [1], Maciej Pabijan [2], Walter Durka [1], Jacek Radwan [3]

[1] *UFZ Leipzig-Halle, Department of Community Ecology, Theodor-Lieser-Str. 4, 06120, Halle, Germany*
[2] *Jagiellonian University, Department of Comparative Anatomy, Ingardena 6, 30-060, Krakow, Poland*
[3] *Jagiellonian University, Institute of Environmental Sciences, Theodor-Lieser-Str 4, 06120, Krakow, Poland*

wieslaw.babik@ufz.de

Patterns of MHC evolution and variation in non-mammalian vertebrates are poorly known. Particularly, very limited information is available for amphibians, a group declining rapidly worldwide. As infectious diseases are invoked in the declines, information on MHC variation may be important in devising conservation strategies. We determined MHC II and microsatellite variation in two populations of the great crested newt (*Triturus cristatus*) from the postulated refugial area (southern Romania) and two populations from the areas of postglacial expansion (UK and Poland). We tested for signatures of historical positive selection and assessed the relative importance of drift and selection in shaping MHC II variation. We found from two to seven unique MHC sequences per individual, indicating the presence of multiple loci, their number differing between individuals. Sequences clustered into two groups on phylogenetic trees. One group (A), containing the expressed sequence, showed an excess of nonsynonymous substitutions at the antigen binding sites (ABS). The other group (B) was shown to have been evolving either under weak purifying selection or neutrally; it represents either pseudogenes or nonclassical MHC loci. There was a striking contrast in MHC diversity between the expansion and refugial areas with four sequences (two from each group) found in Poland and UK and 25 (15 from the A and 10 from the B group) in southern Romania. Microsatellite variation was also significantly lower in formerly glaciated areas. Thus, MHC II variation, concomitantly to neutral variation, was strongly affected by bottlenecks during postglacial expansion. Despite this, populations in the expansion area have been viable for several thousands of years.

17-04 Poster

MH II GENE DIVERSITY AND ALLELE DISTRIBUTION AMONG TWO SYMPATRIC EURASIAN PERCH (PERCA FLUVIATILIS L.) SUBPOPULATIONS OF LAKE CONSTANCE, GERMANY

Jasminca Behrmann-Godel [1], Christian Michel [1]

[1] *University of Konstanz, Limnological Institute, Mainaustrasse 252, 78457, Konstanz, Germany*

Jasminca.Behrmann@uni-konstanz.de

One major goal of evolutionary biology is to investigate how selection drives local adaptation of organisms to their ambient environment. Finding appropriate genetic markers to address these kinds of questions is fundamental. Genes of the major histocompatibility complex (MHC or MH genes in teleosts) are most suitable for examining selective processes. They are among the most polymorphic genomic regions identified in vertebrates. The high level of MHC polymorphism is explained by parasite and pathogen driven selection and by disassortative mating preferences.We investigated MH II gene diversity in approx. 50 Eurasian perch (*Perca fluviatilis* L.) from two sympatric populations of Lake Constance. Gene fragments, including intron1 and most of exon2 of the MH II ß domain were amplified, subcloned and sequenced. Data analyses revealed more than 30 unique exon2 sequences, with up to ten different sequences within a single individual. The rate of nonsynonymous changes (d_N) exceeded the rate of synonymous changes (d_S) at the putative peptide binding region of exon2, indicating that balancing selection maintains diversity of MH II genes, which is also known from many other vertebrates. Whereas some of the exon2 alleles were present in almost all individuals, others were private to one of two sympatric populations. Intron 1 sequences were between 326 and 721bp in length and consisted mainly of a 77bp sequence repeat, with differing repeat numbers and slight sequence variations.

Our study shows substantial variability and the presence of multiple MH II gene loci in Eurasian perch. The suggested difference in allele composition among the two subpopulations indicate that MH II genes may play a role for local population sub structuring, which could be mediated by assortative mating decisions due to preference for population-specific MH II alleles. This ongoing process could promote cladogenesis and finally speciation.

17-05 Poster

OWLS (STRIGIFORMES) CHALLENGE THE PRESENT VIEW OF AVIAN MHC EVOLUTION

Reto Burri [1], Helene Niculita [1], Alexandre Roulin [1], Luca Fumagalli [1]

[1] *University of Lausanne, Laboratory for Conservation Biology, Department of Ecology and Evolution, Biophore, CH-1015, Lausanne, Switzerland*

reto.burri@unil.ch

The major histocompatibility complex (MHC) represents a highly variable multi-gene family critical to the vertebrate immune system. Despite many elements of conserved structure and function, MHC evolution in some lineages was found to differ from well-defined mammalian norms. In most taxa, including mammals, genes of related species form orthologous clusters, following a birth-and-death model of evolution. In birds however, so far orthologous relationships have been revealed only twice, indicating elevated rates of concerted evolution or recent duplication.

To shed light on the time scale at which the diversification and homogenization of avian MHC genes occur, we isolated exon 2 and exon 3 sequences of MHC class II B (MHCIIB) genes in fourteen species of owls (Strigiformes). Exon 2 encodes the β1-domain involved in antigen binding and is supposed to be under balancing selection, while exon 3 contains the β2-domain involved in T-cell binding.

Our analyses reveal that the regions of owl MHCIIB exon 2 involved in antigen-binding are under positive selection, while non-antigen-binding sites are under purifying selection. Moreover, they show that exon 2 sequences might be shuffled between loci. Phylogenetic reconstructions on owl MHCIIB exon 3 demonstrate for the first time the retention of an ancestral MHC polymorphism within and between avian orders over at least 75 MYA. . This appears a magnitude of a time scale longer compared to the two only cases of orthology revealed in the avian MHC, dating 4 MYA and 20 MYA, especially as in these species inference of orthology is based on non-coding sequences. Finally, patterns of evolution in nocturnal raptors appear to largely recall patterns of MHC evolution in non-avian lineages, and challenge the present view of avian MHC evolution.

17-06 Poster

THE IMPACT OF RECOMBINATION ON THE ESTIMATES OF SELECTION IN MHC

Jose L. Campos [1], Antonio Carvajal-Rodríguez [2], Paloma Morán [2], David Posada [2]

[1] *Institute of Wildlife Ecology, Savoyenstraße 1, 1160, Vienna, Austria*
[2] *Universidad de Vigo, Bioquímica, Genética e Inmunología, Facultad de Ciencias. Lagoas-Marcosende, Vigo, Spain*

Jose.Campos@fiwi.at

Genetic variation at the Major Histocompatibility Complex (MHC) is a recurrent theme in conservation genetics, as these genes represent some of the best candidates to study molecular adaptation. In natural populations screened for the MHC, it is common to estimate the ratio of nonsynonymous/synonymous substitution rates (dN/dS) to detect the footprint of natural selection. Positive selection ($dN/dS > 1$) has been detected in MHC in many natural populations. However, recombination is very common in MHC, and it is known that this situation can lead to the overestimation of the dN/dS ratio. Very recently, Wilson and McVean (2006) have proposed an estimator of the dN/dS ratio that is not affected by recombination. Here we compare this and more traditional approaches to estimate the dN/dS ratio, which ignore recombination, in the MHC of an Atlantic salmon population. The main question we want to address is whether traditional methods seem to overestimate dN/dS as a consequence of recombination. To confirm the trends that we have observed with the analysis of empirical data we will also perform computer simulations. We will parameterize these simulations with the estimates of the recombination rate and dN/dS calculated with the method of Wilson and McVean (2006) from the salmon MHC data, and compare how precisely the different methods estimate dN/dS.

17-07 Poster

MHC VARIATION IN THE HOUSE MOUSE HYBRID ZONE

Dagmar Cizkova [1], Joelle Gouy de Bellocq [2], Tomas Albrecht [1], Milos Macholan [3], Jaroslav Pialek [1], Josef Bryja [1]

[1] *Department of Population Biology, Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, Studenec, Czech Republic*
[2] *Research Institute of Wildlife Ecology,University of Veterinary Medicine, Vienna, Austria*
[3] *Laboratory of Mammalian Evolutionary Genetics, Institute of Animal Physiology and Genetics, ASCR, Brno, Czech Republic*

dejsha@seznam.cz

The hallmark of MHC genes is the extremely high degree of polymorphism. This polymorphism is believed to reflect the ability of immune system to respond to a broad spectrum of pathogens and to face the pathogens changing in time. In this study we focused on natural house mouse populations from a hybrid zone between two subspecies, Mus musculus musculus and M. m. domesticus. In central Europe, these genetically diversified subspecies meet and hybridize, which allows gene flow between them. Our aim was to compare the MHC variability in parental mice genomes and the distribution of alleles across the hybrid zone. We examined 285 individuals from 13 populations for polymorphism of the second exon of the MHC class II DRB (H2-Eb1) gene. Mice were genotyped by capillary SSCP method with further characterisation of alleles by the cloning-sequencing approach. We found 12 DRB alleles occurring in the populations. Frequencies of the two most common alleles exceeded 50% and 17%, respectively. These alleles showed even distribution across the hybrid zone, with one of these alleles occurring in every population tested. This result could reflect presence of a pathogen species (strain) common to both subspecies, making them genetically homogenous by its selective pressure. On the other hand, at least 6 alleles (frequencies from 0.2% to 5%) showed clear specificity with respect to musculus or domesticus side of the hybrid zone. We suppose that this differentiation could be maintained by the presence of a locally specific pathogen.

17-08 Poster

MHC-MEDIATED MATE CHOICE INCREASES PARASITE RESISTANCE IN SALMON

Sofia Consuegra [1], Carlos Garcia de Leaniz [1]

[1] *University of Wales Swansea, Biological Sciences, Singleton Park, SA2 8PP, Swansea, UK*

s.consuegra@swansea.ac.uk

The importance of indirect genetic benefits (potential benefits for the offspring) in the evolution of mate choice is a contentious issue. Natural (parasite-driven) and sexual selection are supposed to maintain the high polymorphism of the genes form the Major Histocompatibility Complex (MHC). Females seem to choose mates that optimize the MHC variability of the offspring, in order to increase their ability to defend from a broad number of pathogens. Being heterozygous for MHC or carrying rare alleles can confer the individual an immunological advantage in the response to parasite infections. There is however, only limited evidence of a link between the benefits of MHC-mediated mate choice and the MHC-related response to parasites. Here we tested the existence of this link by comparing MHC individual diversity and parasite loads in the offspring of wild (free mating) and artificially spawned (deprived from the potential benefits of mate choice) Atlantic salmon. We found that hatchery-reared salmon had significantly higher parasite loads and lower MHC individual diversity. Moreover, wild salmon infected with parasites had significantly more individual MHC diversity than those not infected. Our results suggest that MHC-mediated sexual selection and natural (parasite-driven) selection can act in combination to maintain MHC diversity.

17-09 Poster

ON THE WAY TO SPECIATION? USE OF IMMUNE GENES (MHC) TO ESTIMATE DIFFERENTIATION OF STICKLEBACKS (GASTEROSTEUS ACULEATUS).

Christophe Eizaguirre [1], Martin Kalbe [1], Tobias Lenz [1], Manfred Milinski [1]

[1] *Max Planck Institute of Evolutionary Biology (Max Planck Institute for Limnology), Evolutionary Ecology, August-Thienemann-Strasse 2, 24306, Ploen, Germany*

eizaguirre@mpil-ploen.mpg.de

Population differentiation is often viewed as an important step towards speciation. Moreover, sexual selection, particularly female choice, appears to reinforce the divergence that natural selection has generated. Thanks to their habitat plasticity (sea, river, lake) and complex mating system, sticklebacks offer an intriguing opportunity to investigate local adaptations and its role in speciation. However, genetic markers that are used in this context should be directly connected to the environment, i.e. should be functional in ecological terms. From their tight association with environmental pressures (parasite fauna), genes of the Major Histocompatibility Complex (MHC) appear to be good candidates for estimating the degree of local adaptation. This is why, based on a yearlong survey, we investigate the influence of immunology and genetics (genomic and cDNA) to explain which barriers prevent fish from switching between habitats and potentially separate the two groups.

17-10 Poster

GEOGRAPHIC STRUCTURE AND LOCAL ADAPTATION IN MHC CLASS II OF THE GREAT SNIPE.

Robert Ekblom [1], Stein Are Sæther [2], Pär Jacobsson [1], Peder Fiske [3], Tobias Sahlman [1], Mats Grahn [4], John Atle Kålås [3], Jacob Höglund [1]

[1] Uppsala University, Population Biology and Conservation Biology, Norbyvägen 18D, 75236, Uppsala, Sweden
[2] Netherlands Institute of Ecology, Centre for Terrestrial Ecology, PO Box 40, 6666 ZG, Heteren, The Netherlands
[3] Norwegian Institute for Nature Research, Tungasletta 2, N-7485, Trondheim, Norway
[4] Södertörn University College, Molecular Ecology, PO Box 4101, 14104, Huddinge, Sweden

robert.ekblom@ebc.uu.se

The genes of the MHC (major histocompatibility complex) code for proteins involved in antigen recognition and triggering of the adaptive immune response, and are therefore likely to be under selection from parasites. The exact nature of this selection has however been debated for centuries with focus on how polymorphism in the MHC is maintained. One possibility that have not been much explored is that selection regimes may vary in space and time. We have found strong geographic structure in MHC class IIB genes of a migrating bird, the great snipe (*Gallinago media*). Genetic differentiation in the MHC between two ecologically distinct distributional regions was still present after statistically controlling for the effect of selectively neutral variation (microsatellites) using partial Mantel tests. This suggests a role for selection in generating this spatial structure and that it represents local adaptation to different environments. Differentiation between populations within the two regions was negligible. Overall, we found a high number of MHC alleles (50, from 175 individuals). This, together with a tendency for a higher rate of nonsynonymous than synonymous substitutions in the peptide binding sites, and high Tajima's D in certain regions of the gene, suggests a history of balancing selection. MHC variation is often thought to be maintained by some form of balancing selection, but the nature of this selection remains unclear. Our results support the hypothesis that spatial variation in selection regimes contributes to the high polymorphism.

17-11 Poster

INFLUENCE OF GENETIC DISSIMILARITY IN THE REPRODUCTIVE SUCCESS AND MATE CHOICE OF BROWN TROUT

Lars Forsberg [1], Mats Grahn [1]

[1] Södertörn University College, School of Life Sciences, Alfred Nobels Alle 3, 41489, Huddinge, Sweden

lars.forsberg@sh.se

The genes of the major histocompatibility complex (Mhc) are involved in antigen presentation in the immune system where they play a major role in individuals defence against an evolving pathogenic fauna. Studies on species such as mice, human and sticklebacks have revealed that Mhc-genes could be involved in the process of mate choice as well.

This study estimates the influence of genetic dissimilarity at one Mhc class IIB and 11 neutral loci in the mate choice of brown trout (Salmo trutta L.). We examined the reproductive success of 48 adult individuals reproducing in a stream controlled for the absence of other trout. Parentage analysis based on the microsatellites allowed us to infer reproductive success and mate choice preferences in situ. We found that pairs of intermediate Mhc dissimilarity, estimated as average amino acid sequence divergence, mated more often than expected from random mating. It appears that female choice was the driving force behind this observation, since compared to other individuals males with intermediate Mhc dissimilarity produced a larger proportion of offspring, whereas female reproductive output did not show this pattern. Hence, rather than seeking mates with maximal Mhc dissimilarity as found in several species, we found that brown trout prefer mates of intermediate Mhc difference, thus supporting a optimality based model for Mhc based mate choice.

17-12 Poster

PATTERNS OF EVOLUTION IN RELATION TO MHC VARIATION AMONG CORVIDS

Peter Halvarsson [1], Jan Ekman [1]

[1] *Ecology and Evolution, Population Biology and Conservation Biology, Norbyvägen 18D, 752 36, Uppsala, Sweden*

peter.halvarsson@ebc.uu.se

Sequence variation is widely used to investigate mechanisms of evolution. So far, few bird species, mostly passerines and galliformes, have been analyzed for *MHC* variation. With the exception of the Scrub Jay, corvids have not been investigated. As *MHC* molecules present pathogens to T cells, which activate the immune response, the *MHC* is thought to be under balancing selection imposed by pathogens. We are planning to contrast *MHC* variation with the biogeography of corvids. The aim to investigate evolutionary patterns in life history in relation to *MHC* variation in this group of birds. We have successfully amplified a fragment of the *MHC* class II β in a set of species. The fragments show a high similarity to already published *MHC* sequences from other birds.

17-13 Poster

MHC POLYMORPHISM AS A TOOL IN RAINBOW TROUT BREEDING

Mette H. H. Hansen [1], Mark A. Henryon [1]

[1] *University of Aarhus, Faculty of Agricultural Sciences, Blichers Allé 20, Postboks 50, DK8830, Tjele, Denmark*

metteh.hansen@agrsci.dk

We are investigating how MHC polymorphism contributes to genetic variation for disease resistance, in order to employ this in our breeding strategy for improved resistance in farmed rainbow trout. We have previously demonstrated that additive genetic variance is present for resistance to three major pathogens to farmed rainbow trout, enteric redmouth disease, rainbow trout fry syndrome, and viral haemorrhagic septicaemia. Salmonid MHC has a uniquely minimalistic genetic architecture with just one locus coding for the classical MHCI molecule, and one locus coding for each of the α and β chains of MHCII. This enables us to obtain complete information on the peptide binding properties of the MHC in our trout by sequencing these loci. We combine a quantitative genetic mating design with complete information on polymorphisms in the peptide binding regions of classical MHCI and MHCII loci to obtain offspring fish with family specific allele combinations. By subjecting these fish to challenge experiments with enteric redmouth disease, rainbow trout fry syndrome, and viral haemorrhagic septicaemia, we can quantify the relative contributions of additive genetic variance as well as direct MHC allele- and genotypes to pathogen resistance. Having complete sequence information of the classical MHC regions in our parent fish allows us to construct allele phylogenies and to estimate the force of positive selection on our farm trout population both long term (by dN/dS ratios) and short term (by allele frequencies). The combined information on challenge experiments, quantitative genetic effects and direct MHC effects is used to design a strategy for breeding rainbow trout for resistance to disease.

17-14 Poster

MOLECULAR CHARACTERIZATION OF MHC CLASS II IN A NON-MODEL ANURAN SPECIES, THE FIRE-BELLIED TOAD BOMBINA BOMBINA

J. Susanne Hauswaldt [1], Simone Pfautsch [2], Heiko Stuckas [2], Ralph Tiedemann [2]

[1] *University of Cologne, Evolutionary Biology, Zuelpicher Str. 47, 50674, Cologne, Germany*
[2] *University of Potsdam, Evolutionary Biology/Systematic Zoology, Karl-Liebknecht-Str. 24-25, 14476, Potsdam, Germany*

shauswal@uni-koeln.de

The organization of the major histocompatibility complex (MHC) has never been studied in any anurans other than *Xenopus*. We have characterized MHC class II B cDNA sequences from a non-model anuran species, the European fire-bellied toad (*Bombina bombina*). We isolated two transcript sequences differing substantially in amino acid composition and length within the β2 domain. We have also sequenced a 158 bp large fragment from wild *B. bombina* (N = 20) and identified eight distinct alleles. Many of the highly polymorphic sites corresponded with antigen binding sites. We conclude that *Bombina* possesses at least two class II B loci based on the cDNA data and the individual's allelic diversity. Our new β1 primers cross-amplified in other species of anurans, and we are presenting a phylogenetic analysis of this gene in amphibians.

17-15 Poster

AN INCREASE IN PH BOOSTS OLFACTORY COMMUNICATION IN STICKLEBACKS

Jan Heuschele [1], Ulrika Candolin [2]

[1] *University of Helsinki, Department of Biological and Environmental Sciences, Viikinkaari 1 PO Box 65, 00014, Helsinki, Finland*
[2] *Uppsala University, Department of Ecology and Evolution/Limnology, PO Box 573, 75123, Uppsala, Sweden*

jan.heuschele@helsinki.fi

Human induced eutrophication is a serious environmental problem. It constrains visual communication, reduces the honesty of sexual signalling, and influences the mate choice process in fishes. Eutrophication also changes the chemical environment and the pH of the water, which could influence the use of olfactory cues in mate choice. Here we show that an increase in pH enhances the use of male olfactory cues in mate choice in threespine sticklebacks Gasterosteus aculeatus. In a laboratory choice experiment, ripe females were more attracted to male olfactory cues when pH was raised. Especially since those cues are known to give females information on the allele diversity at MHC genes, this could compensate for impaired visual communication in eutrophicated waters and facilitate adaptive mate choice.

17-16 Poster

MHC, COLOURS AND PARASITISM IN AN ARCTIC CHARR, SALVELINUS ALPINUS, POPULATION

Jukka Kekäläinen [1], Albert Vallunen [2], Craig Primmer [2], Jouni Taskinen [1]

[1] *University of Joensuu, Ecological Research Institute, P.O. Box 111, FI-80101, Joensuu, Finland*
[2] *University of Turku, Depertment of Biology, FI-20014, Turku, Finland*

jkekalai@cc.joensuu.fi

The Arctic charr, Salvelinus alpinus, have a distinct red abdominal colouration which may have evolved and maintained via sexual selection. According to the "complementary resistance genes" hypothesis, females should benefit from mating with males having favourable MHC profiles. To test the hypothesis, we studied MHC genotype, parasitism and colours of the wild charrs, collected from Lake Peltojärvi, Northern Finland, in April 2006. Fish had low MHC IIβ variation with only two alleles in the studied locus. In accordance with the hypothesis, results of ANCOVA indicated that MHC-homozygotes ($n = 10$) had significantly higher mean abundance of tissue-encysted *Diphyllobothrium* (Cestoda) larvae as compared to MHC-heterozygotes ($n = 8$). There was also a statistically significant negative correlation between carotenoid based redness of the muscle and the number of *Diphyllobothrium* in the muscle, a negative correlation between skin and muscle redness, and a positive correlation between skin redness and the total number of *Diphyllobothrium*. Finally, in this sample collected outside the breeding period, there was a trend for brighter red colouration in MHC-homozygotes than in heterozygotes.

17-17 Poster

MAJOR HISTOCOMPATIBILITY GENES AND PARASITE LOAD IN WILD BANK VOLE

Agnieszka Kloch [1], Anna Bajer [2], Edward Siński [2], Wiesław Babik [1], Jacek Radwan [1]

[1] *Jagiellonian University, Institute of Environmental Sciences, ul. Gronostajowa 7, 30-387, Krakow, Poland*
[2] *Warsaw University, Department of Parasitology, ul. Miecznikowa 1, 02-096, Warszawa, Poland*

akloch@eko.uj.edu.pl

MHC genes, coding for proteins involved in immune response, are among the most polymorphic loci in vertebrates. The parasites are thought to be the major evolutionary force maintaining high MHC diversity.. To assess the role of MHC genes in determining susceptibility to parasites in the wild we examined three bank vole populations in north-eastern Poland. We identified intestinal parasites (helminths and protozoa) in necropised animals. The voles were genotyped at the second exon of MHC DRB (class II) genes. The parasite community and frequency of DRB alleles differed between the populations, We found significant, population-specific associations between particular alleles and infection intensity and/or prevalence. Our results indicate that parasites affect frequencies of MHC alleles in the wild and that selection differs in space.

17-18 Poster

EVOLUTION OF ADAPTIVE IMMUNE GENES IN TWO SYMPATRIC STICKLEBACK SPECIES (G. ACULEATUS & P. PUNGITIUS)

Tobias L. Lenz [1], Christophe Eizaguirre [1], Manfred Milinski [1]

[1] *Max Planck Institute for Evolutionary Biology, Dept. of Evolutionary Ecology, August-Thienemann-Str. 2, 24306, Plön, Germany*

lenz@post.harvard.edu

Adaptation is needed to persist in a given environment, including resistance to common pathogens. Vertebrates possess an adaptive immune system, which enables them to both recognize specific pathogens and trigger a respective response upon recognition as well as build up a memory to prevent future invasions. The Major Histocompatibility Complex (MHC) is part of this adaptive immune system. Most of its genes show outstanding polymorphism in terms of allelic and genetic diversity, which has presumably evolved to confer resistance against the nearly infinite diversity of pathogens. Interactions between distinct MHC alleles and groups or even species of pathogens have been observed. We therefore assume host populations to differ in their respective MHC allele repertoire if they are facing different pathogen spectra. Sticklebacks show both high MHC allele diversity within individuals, but also within and between populations. Here we study the MHC constitution of two sympatric species, the three-spined and the nine-spined stickleback, that co-occur in different habitats (lake, river and estuary) and share several macroparasites within each respective habitat.

17-19 Poster

MHC VARIATION IN BUFO CALAMITA

Shoshanna May [1], Inga Zeisset [1], Trevor Beebee [1]

[1] *Univeristy of Sussex, Life sciences, Falmer, Brighton, England*

sm57@sussex.ac.uk

The global decrease of amphibian populations is a matter of great international concern. There is increasing evidence for the hypothesis that pathogens have been important contributors to amphibian population declines in many different parts of the world. Major histocompatability complex (MHC) proteins are critical components of the cellular immune response and MHC class II loci are interesting because they encode cell-surface proteins that bind antigens and play crucial roles in disease resistance. MHC proteins have previously been characterised in *Xenopus laevis* and *Ambystoma mexicanum*. Here we present the results of a study looking at sequence variation in *Bufo calamita* MHC class II Beta exon 2.

17-20 Poster

PATHOGEN-DRIVEN SELECTION ON THE MHC IN TWO MARSUPIALS FROM THE BRAZILIAN ATLANTIC RAINFOREST

Yvonne Meyer-Lucht [1], Celine Otten [1], Thomas Puettker [1], Simone Sommer [1]

[1] *Leibniz Institute for Zoo and Wilflife Research, Evolutionary Genetics, Alfred-Kowalke-Str. 17, 10315, Berlin, Germany*

meyerlucht@izw-berlin.de

The central role of the major histocompatibility complex in terms of pathogen defense is undoubted. The remarkable MHC diversity found in nearly all vertebrate studies to date refers to diversifying selection acting on this gene complex. There is evidence for the hypothesis that high pathogen diversity exposure leads to increased MHC variation, whereas low pathogen richness leads to reduced selective pressure on MHC diversity.

To test this hypothesis, we investigated the intestinal parasite load and the MHC II *DRB* variation in two neotropical marsupials, *Marmosops incanus* and *Gracilinanus microtarsus,* endemic to the Brazilian Atlantic Rainforest. Both species are common in this region and depend on forest habitats, but differ in their gastrointestinal parasite diversity. In *M. incanus*, the gastrointestinal parasite fauna is dominated by a single nematode species accounting for 95% of the infections. However, in *G. microtarsus*, three different helminth species are accounting for 90% of the infections. These different challenges seem to be reflected by the MHC constitution of the species: *M. incanus* has a very low MHC *DRB* variation, while *G. microtarsus* displays an extensive MHC *DRB* variability in terms of the number of alleles and sequence variation. Our results support the initially mentioned hypothesis that high pathogen diversity leads to an increased MHC diversity. These results might have important ecological consequences, as both species differ in their sensitivity to habitat fragmentation. Their habitat, the coastal Atlantic Rainforest, is largely destroyed and still being fragmented. Implications for conservation are discussed.

This study was carried out within the project Mata Atlântica, which aims to develop concepts for the conservation of the biodiversity in the region of the Atlantic Rainforest in Brazil. With kind support by the BMBF Germany.

17-21 Poster

EVOLUTION OF MHC CLASS I GENES IN REPTILES: ALLELIC DIVERSITY AND MATE CHOICE IN TUATARA (SPHENODON PUNCTATUS).

Hilary C. Miller [1], Jennifer A. Moore [1], Charles H. Daugherty [1]

[1] *Victoria University of Wellington, School of Biological Sciences, PO Box 600, 6140, Wellington, New Zealand*

hilary.miller@vuw.ac.nz

Much of what we know about the evolution of MHC genes comes from studies of fish, birds and mammals. These studies show striking differences between the major vertebrate groups in MHC organisation, and in how diversity at MHC genes is generated and maintained. However, few studies have analysed MHC evolution in reptiles, despite their important phylogenetic position as sister taxa to both mammals and birds. We have analysed variation at MHC class I genes in a large population of an archaic reptile species, the tuatara (*Sphenodon punctatus*). Tuatara are the sole extant species in the order Sphenodontia, the sister group of squamates (lizards and snakes). We have isolated at least two highly polymorphic MHC class I genes from tuatara, and investigated the evolutionary processes that generate and maintain MHC diversity. Allelic diversity is generated by a mixture of point mutation and gene conversion. As has been found in birds and fish, gene conversion obscures the genealogical relationships among alleles and prevents the assignment of alleles to loci. We have also investigated the role of mate choice in maintaining high levels of MHC diversity and will present preliminary data from this study.

17-22 Poster

TESTING HYPOTHESES ON MHC GENETIC VARIATION: CLASSICAL AND NEW METHODS WITH APPLICATIONS

Stefano Mona [1], Aldo Solari [2], Livio Finos [3], Giorgio Bertorelle [1]

[1] University of Ferrara, Biology and Evolution, Via L. Borsari 46, 44100, Ferrara, Italy
[2] University of Padova, Statistics, Via 8 Febbraio 2, 35122, Padova, Italy
[3] University of Ferrara, Biomedical Sciences, Corso Giovecca 203, 44100, Ferrara, Italy

stifano1@yahoo.it

Here we review and compare different statistical methods generally used to study the MHC inter- and intra-specific polymorphisms. We specifically consider the relative influence of the demographic history and the different selective processes on these methods, discussing also the role that the additional analyses of neutral markers has to better understand the MHC genetic variation. The possibility to detect the selection process on specific alleles or amino acids, or in specific populations, or groups of individuals with specific phenotypes, is then investigated using a general approach based on the nonparametric combination of the p-values obtained in several non-independent tests. This approach controls efficiently the type I errors, by taking into account the dependence structure among tests. The different methods are applied to a real case of MHC and microsatellite data available for two chamois species.

17-23 Poster

MHC DIVERSITY AND MATE CHOICE IN WILD HOUSE MICE (MUS MUSCULUS MUSCULUS)

Kerstin Musolf [1], Katrin Rödlach [1], Dustin J. Penn [1]

[1] Konrad Lorenz-Institute for Ethology, Austrian Academy of Sciences, Savoyenstr. 1A, A-1160, Vienna, Austria

k.musolf@klivv.oeaw.ac.at

To evaluate how the exceptional high polymorphism of the MHC is maintained in wild populations we compared MHC-linked microsatellite markers with neutral microsatellite markers to determine different selective pressures in four different wild mouse populations over time. Preliminary data reveal different selective pressures acting on MHC-linked and neutral markers, but surprisingly no strong population differentiation has been found. MHC-disassortative mating preferences are thought to be one potential mean to maintain MHC polymorphism by increasing the resistance of an individual's offspring to parasites or as a genetic kin recognition system to avoid inbreeding. Therefore, we tested whether MHC-disassortative odor and mating preferences occur in wild house mice. Estrus females were tested in a two-choice apparatus for odor preference using male scent marks as stimulus cue. While females significantly preferred the odor of unfamiliar unrelated males versus unfamiliar brothers – a clear indication of inbreeding avoidance, this preference was reversed when tested against a familiar brother. Further, we tested actual mating preferences using collared males and free moving females. Observational data and genetic paternity analyses of offspring indicated no mating preference raising the question whether mate choice plays a role in maintaining MHC polymorphism in this species.

17-24 Poster

MHC POLYMORPHISM: DOES DOMINANCE FOR RESISTANCE TO PATHOGENS MAKE THE DIFFERENCE?

Maciej Ejsmond [1], Maciej Dańko [1], Jacek Radwan [1]

[1] Jagiellonian University, Institute of Environmental Sciences, ul. Gronostajowa 7, 30-387, Krakow, Poland

radwan@eko.uj.edu.pl

MHC diversity is thought to be driven by mainly by parasites. High polymorphism of these genes has been hypothesized to arise from heterozygote advantage and/or frequency-dependence arising from host-parasite coevolution. The advantage of heterozygotes will depend on the degree of the dominance for resistance conferred by MHC alleles. We simulate host-parasite coevolution under varying degree of dominance for resistance. We find that the number of MHC alleles maintained in populations increases with dominance. Our model also shows that distribution of MHC allele frequencies depends on the dominance for the resistance to pathogens. This last result has implications for detection of selection on MHC using tests based on allele frequencies.

17-25 Poster

MHC AND REPRODUCTIVES SUCCESS IN FIELD POPULATION OF THE BANK VOLE

Jacek Radwan [1], Wiesław Babik [1], Zbigniew Boratyński [1]

[1] Jagiellonian University, Institute of Environmental Sciences, ul Gonostajowa 7, 30-387, Krakow, Poland

radwan@eko.uj.edu.pl

While the evidence for associations of MHC alleles with infections is increasing, it is not clear how such associations translate into selection in natural populations. We released 56 bank adult voles released on an island on Solina lake, SE Poland. Their survival was monitored and genetic samples of the next generation were collected. Reproductive success was assigned using 6 microsatellite loci. Second exon of the MHC class II DQB locus was amplified and genotype assigned using SSCP. We will present analyses of associations between MHC and survival and reproductive success of the released individuals.

17-26 Poster

CONSTRAINTS ON THE ORIGIN AND MAINTENANCE OF GENETIC KIN RECOGNITION

Francois Rousset [1], Denis Roze [2]

[1] CNRS & University Montpellier 2, Institut des Sciences de l'Evolution, CC065 ISEM USTL Pl. E. Bataillon, 34095, Montpellier, France
[2] CNRS, Station biologique de Roscoff, Pl. G. Teissier, 29680, Roscoff, France

rousset@isem.univ-montp2.fr

Kin recognition mechanisms allow helping behaviors to be directed preferentially toward related individuals, and could be expected to evolve in many cases. However, genetic kin recognition requires a genetic polymorphism on which recognition is based, and kin discriminating behaviors will affect the evolution of such polymorphism. It is unclear whether genetic polymorphisms used in kin recognition (such as MHC polymorphism) should be maintained by extrinsic selection pressures or not, as opposite conclusions have been reached by analytical one-locus models and by simulations exploring different population structures. We analyze a two-locus model in a spatially subdivided population. We demonstrate a continuum of situations, with extrinsic selection being necessary in most cases except with extreme spatial structure and low recombination. Our results indicate similar constraints for the evolution of recognition polymorphisms as a means to avoid germ line parasitism. Available evidence for extrinsic selection on recognition polymorphisms beyond the MHC is reviewed.

17-27 Poster

VARIABLE DIVERSITY AND EXPRESSION OF MHC CLASS II B AND Y GENES IN BLACK GROUSE (TETRAO TETRIX).

Tanja Strand [1], Helena Westerdahl [2], Jacob Höglund [1], Rauno Alatalo [3], Heli Siitari [3]

[1] Uppsala University, Dep. of Ecology and Evolution, Population Biology and Conservation Biology, Norbyvägen 18D, SE-75236, Uppsala, Sweden
[2] Lund University, Dep of Animal Ecology
[3] University of Jyväskylä, Dep of Biological and Environmental Science

Tanja.Strand@ebc.uu.se

We found that the Major histocompatibility complex (*Mhc)* class II beta (B) organisation of the lek-breeding galliform bird species Black grouse resemble the *Mhc* of the domestic chicken (*Gallus gallus*). *Mhc* class IIB in both chicken and Black grouse consists of two clusters of genes, the B and Y genes, that differ in diversity and expression. The Black grouse B genes showed the same level of polymorphism that has been reported in chicken and other vertebrates. The Y genes showed less variation, also in accordance with studies on chicken. The functional significance, if any, of the Y genes remain obscure. However, our expression studies indicate that the B genes are expressed and involved in the immune defence. We hypothesize that the Y genes have been under purifying selection, just as the mammal *Mhc*-E gene cluster. The number of *Mhc* class IIB loci in Black grouse appears to be low, probably consisting of two B and two Y loci, respectively. This suggests Black grouse has a “minimal essential *Mhc*” like the chicken. Molecular information available for avian *Mhc* genes is increasing but a better taxonomic coverage is needed to understand the evolution of *Mhc* genes. This study provides evidence that the *Mhc* genes of a wild galliform bird are strikingly similar to another galliform: the domestic chicken, and suggests that the *Mhc* organisation of the chicken is not unique among the Galliform species.

17-28 Poster

GENETIC COMPATIBILITY, MHC-DISSORTATIVE MATING PREFERENCES AND GENETIC VARIATION IN SMALL POPULATIONS

Hanna Thörngren [1]

[1] *Uppsala university, Animal Ecology, Dept. of Ecology and Evolution, Evolutionary Biology Centre, Norbyvägen 18D, SE-752 36, Uppsala, Sweden*

hanna.thorngren@ebc.uu.se

The Major Histocompatibility Complex (MHC) is a cluster of genes that play a major role in the immune defence in vertebrates, it recognises foreign peptides and triggers the right immune responses. The MHC shows a very high degree of polymorphism in natural populations. One way of explaining this pattern is by balancing selection maintained by sexual selection. A preference for dissimilar genes at the MHC would enhance MHC diversity and overall heterozygosity in offspring, making them capable of fighting a wider range of parasites. In small populations, prone to inbreeding, MHC dissortative mating preferences may be a way to avoid inbreeding depression. The hybrid zone of flycatchers on the island of Öland is a good study system for investigating whether there is a link between MCH dependant mating patterns and genetic variation observed at the population level. Collared flycatchers colonized Öland as late as in the 70's and breed in comparatively small numbers at certain places. This situation increased both the likelihood of inbreeding and out breeding (i.e. hybridization with the closely related pied flycatcher). I will discuss the advantage of using Reference Strand-Mediated Conformational Analysis (RSCA) to determine the MHC genotype of individuals and present some preliminary results supporting mate choice based on genetic compatibility.

17-29 Poster

THE AVIAN MALARIA INFECTION WITH HIGHEST PEAK PARASITEMIA IS ASSOCIATED WITH THE COMPOSITION OF MHC ALLELES IN GREAT REED WARBLERS.

Helena Westerdahl [1], Pavel Zehtindjiev [2], Bengt Hansson [1], Mihaela Ilieva [2], Gediminas Valkiūnas [3], Staffan Bensch [1]

[1] *Lund University, Animal Ecology, Ecology Building, 22362, Lund, Sweden*
[2] *Bulgarian Academy of Sciences, Insitute of Zoology, Blvd. Tzar Osvoboditel 1, 1000, Sofia, Bulgaria*
[3] *Vilnius University, Institute of Ecology, Vilnius21, LT-08412, Vilnius, Lithuania*

helena.westerdahl@zooekol.lu.se

The high genetic diversity in the Major Histocompatibility Complex (MHC) genes is most likely maintained by selection from a large number of different pathogens. The great reed warbler is host to at least twenty different lineages of avian malaria parasites and is hence a useful study system for investigating balancing selection and associations between MHC genes and disease resistance. We have previously reported of an association between the composition of MHC alleles and resistance to the avian malaria infection *Plasmodium ashfordi* (GRW2) in a wild study population of great reed warblers. This association relies on two assumptions that we made; first that GRW2 is a severe parasite and second that great reed warblers with a certain composition of MHC alleles are more likely to survive such GRW2 infections. In the present study we investigate these assumptions in detail so we took an experimental approach and inoculated juvenile great reed warblers with avian malaria. The experimental birds were subjected to either of three treatments; (a) infected with parasites of lineage GRW2, (b) infected with parasites of lineage *Plasmodium relictum* (GRW4), (c) or not infected. The survival did not differ between the three treatment groups. However, GRW2 showed higher peak of parasitemia than the lineage GRW4 and the mortality of GRW2 infected birds seemed to coincide with rapidly increasing intensities of parasitemia. These results indicate that GRW2 pose a higher fitness cost than GRW4. We also screened the MHC class I genotype of the experimental birds and evaluated whether great reed warblers with a certain composition of MHC alleles have a lower level of parasitemia and suggestively improved probability of survival.

17-30 Poster

SINGLE LOCUS TYPING IN FOWL REVEALS DIFFERENTIAL LEVELS OF DIVERSITY AND SELECTION ACROSS CLASSICAL MHC GENES

Kirsty Worley [1, 2], Mark Gillingham [2], Jim Kaufman [3], Per Jensen [4], Lorna J. Kennedy [5], Tommaso Pizzari [2], David S. Richardson [1]

[1] *University of East Anglia, School of Biological Sciences, NR4 7TJ, Norwich, United Kingdom*
[2] *University of Oxford, Department of Zoology, OX1 3PS, Oxford, United Kingdom*
[3] *Institute of Animal Health, RG20 7NN, Compton, United Kingdom*
[4] *University of Linköping, Department of Biology, SE-581 83, Linköping, Sweden*
[5] *University of Manchester, Centre for Integrated Genomic Medical Research, M13 9PT, Manchester, United Kingdom*

k.worley@uea.ac.uk

The MHC regions of many species comprise several multigene families. In non model species, where molecular gene organisation remains uncharacterised, this necessitates the use of multilocus estimates of MHC diversity. The well characterised 'minimal essential' chicken MHC region, comprising two differentially expressed duplicated class I (BF) and two class II (BLB) genes, allows a single locus approach to be taken in fowl. Classical MHC (B locus) diversity was assessed in populations of domestic chickens (*Gallus gallus domesticus*) and their wild ancestors, red junglefowl (*G. gallus*) through a combination of reference strand-mediated conformation analysis (RSCA) and cloning and sequencing. As expected, the presence of an excess of non-synonymous substitutions, higher levels of heterozygosity than expected under neutrality and the sharing of allelic lineages between taxa suggest the actions of diversifying selection. However the single locus approach reveals that the actions of selection can be partitioned to one locus alone, the more highly expressed copy of BF. Our findings illustrate how pooling alleles across loci reduces the ability to detect processes acting to maintain diversity in natural populations.

17-31 Poster

MHC CLASS II LOCI IN RANA TEMPORARIA

Inga Zeisset [1], Trevor J. C. Beebee [1]

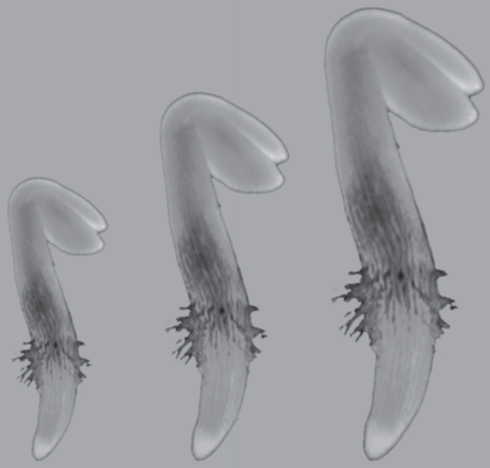
[1] *University of Sussex, School of Life Sciences, Falmer, BN19QG, Brighton, UK*

I.Zeisset@sussex.ac.uk

The causes of amphibian declines pose a major challenge to Biologists worldwide. Apart from habitat destruction, climate change and pollution one of the major causes is disease, especially fungal infections. We present results from a study that aims to characterize exon 2 of the MHC (major histocompatibility complex) class II beta locus of the amphibian *Rana temporaria*. This is the most variable part of the MHC class II and has been shown to be important for triggering immune responses against extra cellular antigens, such as fungal infections.

The origins and spread of agriculture: an evolutionary perspective

18



Saturday August 25 *Location*: University building IX

Symposium 18: The origins and spread of agriculture: an evolutionary perspective

ORGANIZERS: Terry Brown, University of Manchester, UK
Martin Jones, University of Cambridge, UK

9.45-10.15	**Wayne Powell** (invited) Evolution and domestication of crop plants: new insight from population-based re sequencing of candidate genes
10.15-10.45	**Robin Allaby** (invited) Modelling approaches with multilocus systems and the origins of agriculture
10.45-11.05	**Huw Jones** Diversity of the photoperiod response gene Ppd-H1 in European barley and evidence for the origins of an adaptive trait
11.05-11.35	*Coffee*
11.35-11.55	**Hazel Goodwin** The Evolution and Spread of Triticum aestivum in Europe
11.55-12.15	**Jennifer Cunniff** Response of wild C4 crop progenitors to subambient CO2 highlights a possible role in the origin of agriculture
12.15-12.35	**Thure Hauser** Hybridization and evolution between cultivated plants and wild relatives
12.35-12.55	**Anna Westerbergh** Genetic and phenotypic changes in the evolution of the tropical crop cassava (Manihot esculenta spp. esculenta)
12.55-14.00	*Lunch*

18-01 Talk

EVOLUTION AND DOMESTICATION OF CROP PLANTS: NEW INSIGHT FROM POPULATION-BASED RE SEQUENCING OF CANDIDATE GENES

Huw Jones [1, 2], Fiona J. Leigh [1], Ian Mackay [1], Lydia M. J. Smith [1], James Cockram [1], Terence A. Brown [2], Wayne Powell [1]

[1] *NIAB, Huntingdon Rd, Cambridge, CB3 0LE, UK*
[2] *University of Manchester, Manchester Interdisciplinary Biocentre, Faculty of Life Sciences, Manchester, M1 7DN, UK*

wayne.powell@niab.com

Understanding the processes and mechanisms that underpin the evolution and domestication of crop plants represents a major new scientific frontier. The domestication of food plants such as barley and wheat accompanied and, in some cases, were responsible for diffusion of agrarian culture. The evolution and domestication of crop plants had a major impact on societies and civilisations but also resulted in genetic changes in wild plants as cultivated forms were selected. The "domestication syndrome" associated with the selection of key adaptive traits provides an experimental framework to identify nucleotide polymorphisms that are causative. Population based re-sequencing of candidate genes for domestication traits sampled from wild and cultivated germplasm can provide new insights into the process of evolution and domestication.

I will present data on the genomic impact of human-imposed selection that accompanied the domestication of cereals.

18-02 Talk

MODELLING APPROACHES WITH MULTILOCUS SYSTEMS AND THE ORIGINS OF AGRICULTURE

Robin G. Allaby [1]

[1] *University of Warwick, Warwick HRI, Wellesbourne, CV35 9EF, Warwick, United Kingdom*

r.g.allaby@warwick.ac.uk

Crop origins have been the subject of extensive debate in terms of the number and locality of the underlying domestication events. Genome-wide studies have consistently inferred single origins for crops based on the monophyletic phylogenies of the domesticated varieties. Yet phylogenetic evidence from individual genetic loci suggests multiple origins for some of these crops. Modelling approaches demonstrate that monophyly is an inevitable consequence over time using these types of markers, and surprisingly, that mutiple origins can actually lead to monophyly more rapidly than single domestication events. However, the occurrence of monophyly gives us insights into the nature of the original wild populations brought into cultivation in terms of size and diversity.

18-03 Talk

DIVERSITY OF THE PHOTOPERIOD RESPONSE GENE PPD-H1 IN EUROPEAN BARLEY AND EVIDENCE FOR THE ORIGINS OF AN ADAPTIVE TRAIT

Huw Jones [1], Fiona J. Leigh [1], Lydia M. J. Smith [1], Terence A. Brown [2], Wayne Powell [3]

[1] *NIAB, Centre for Crop genetics Evaluation and Breeding, Huntingdon Road, Cambridge, UK*
[2] *Manchester University, Interdisciplinary Biocentre, Faculty of Life Science, Manchester M17DN, UK*
[3] *NIAB, Directorate, Huntingdon road, Cambridge, UK*

huw.jones@niab.com

Barley is one of the founder crops of agriculture, domesticated in the 'Fertile Crescent' and dispersed into Europe during the Neolithic. The dispersal of cultivated barley from the native range of its wild ancestor's (*Hordeum vulgare* ssp *spontaneum*) required adaptation to novel environments and habitats. We have examined the organisation of the photoperiod response gene *Ppd-H1* in a representative sample of elite cultivars, European barley landraces and *Hordeum vulgare* ssp *spontaneum* accessions. In the elite cultivars and European barley landraces, genotypes predicting a non responsive phenotype (*ppd-H1*) are common. In the landraces, sequence based haplotype variation is distributed in a latitudinal cline, with non-responsive *ppd-H1* alleles predominating in north-western Europe. In *Hordeum vulgare* ssp *spontaneum* accessions, genotypes predicting a responsive phenotype (*Ppd-H1*) predominate. The geographic distribution of *Hordeum vulgare* ssp *spontaneum* accessions with the *ppd-H1* genotype supports the hypothesis that there was a second domestication of barley east of the Fertile Crescent. Implications for the origin and dispersal of the non-responsive form (*ppd-H1*) of the photoperiod response gene are discussed in the context of cultivated barley in Europe

18-04 Talk

THE EVOLUTION AND SPREAD OF TRITICUM AESTIVUM IN EUROPE

Hazel E. Goodwin [1], Terry A. Brown [1]

[1] *University of Manchester, Faculty of Life Sciences, 131 Princess Street, M1 7ND, Manchester, UK*

H.Goodwin@postgrad.manchester.ac.uk

The initial aim of this study is to use single nucleotide polymorphisms to determine how hexaploid bread wheat, *Triticum aestivum*, spread from its point of origin in the Near East into Europe. Using the High Molecular Weight glutenin locus of the D genome, a nested PCR system has been developed and used to amplify almost three hundred landraces of *Triticum aestivum*. Previous research has already used this locus to identify two alleles of bread wheat originating from two areas of the Near East and it is hoped that these groupings will also be apparent in the European samples. These results will be further complemented by analysis of twelve microsatellite loci from the D genome and screening for a deletion in the Ppd gene, and it is hoped that when these results are combined they will provide further insights into the Neolithic transition in Europe.

18-05 Talk

RESPONSE OF WILD C4 CROP PROGENITORS TO SUBAMBIENT CO2 HIGHLIGHTS A POSSIBLE ROLE IN THE ORIGIN OF AGRICULTURE

Jennifer Cunniff [1], Colin P. Osborne [1], Brad S. Ripley [2], Charles Mike [3], Glynis Jones [3]

[1] University of Sheffield, Animal and Plant Sciences, Western Bank, S10 2TN, Sheffield, UK
[2] Rhodes University, Botany Department, Grahamstown 6140, South Africa
[3] University of Sheffield, Archaeology, West Street, S1 4ET, Sheffield, UK

j.cunniff@sheffield.ac.uk

The synchronous origin of agriculture in at least four independent climatic regions at the end of the glacial period (10,000 yrs BP) points to a global limitation for crop domestication. One hypothesis proposes that a rapid CO_2 increase from 180ppm to near 280ppm during deglaciation caused significant increase in growth rates of wild crop progenitors, thereby removing a productivity barrier to their successful domestication. However, early C_4 crops present a challenge to this hypothesis, because they were among the first domesticates, but have a carbon-concentrating mechanism that theoretically makes photosynthesis insensitive to CO_2. We investigated the CO_2-limitation hypothesis using a set of five C_4 and one C_3 crop progenitors from four independent centres of domestication. Plants were grown in controlled environment chambers at glacial (180ppm), postglacial (280ppm) and current ambient (380ppm) CO_2 levels, and phenology, photosynthesis, transpiration, biomass and leaf area were measured. An increase in CO_2 from glacial to postglacial levels caused a significant gain in vegetative biomass of up to 40% in C_4 progenitors. Investigation into the underlying mechanisms showed C_4 photosynthesis to be limited by low CO_2 levels. More significantly, the increase in CO_2 caused a reduced transpiration rate via a decreased stomatal conductance. In combination, these physiological changes confer a large improvement in water use efficiency. Our data provide experimental support for the CO_2-limitation hypothesis, suggesting that these key physiological changes could have greatly enhanced the productivity of wild crop progenitors after deglaciation.

18-06 Talk

HYBRIDIZATION AND EVOLUTION BETWEEN CULTIVATED PLANTS AND WILD RELATIVES

Thure P. Hauser [1]

[1] University of Copenhagen, Department of Ecology, Rolighedsvej 21, DK-1958, Frederiksberg, Denmark

tpha@life.ku.dk

During domestication and breeding, crops have diverged from their wild relatives to become adapted to the agronomic, nutritional, and cultural wishes of man. Despite this divergence, a series of recent studies indicates that many cultivated and wild plants are still able to reproduce with each other, and that hybrids between them sometimes may survive and reproduce under natural conditions, which eventually may lead to the transfer of genes and traits.

In my presentation, I will show examples from oilseed rape, carrot, chicory, and other crop species, to illustrate various degrees of coexistence and compatibility between crops and their wild relatives, different hybridization scenarios, fitness of hybrids in relation to environmental conditions, and possible effects on wild populations. I will further discuss reasons why hybridization and gene transfer to wild populations is, and has been, more common than anticipated just a few years ago: we may simply be better equipped to detect such interactions, weedy relatives and volunteers of crop species may be more common than we thought, hybridization and gene transfer may happen in more diverse ways than often considered, and hybrids may not be as maladpted to conditions in the wild as formerly believed.

Our new knowledge on hybridization between cultivated and wild plants challenges our perception of cultivated plants as very different and isolated from wild plants, and has implications for our view of authenticity and conservation of wild and weedy populations of relatives and of landraces of cultivars.

18-07 Talk

GENETIC AND PHENOTYPIC CHANGES IN THE EVOLUTION OF THE TROPICAL CROP CASSAVA (MANIHOT ESCULENTA SPP. ESCULENTA)

Wilson Castelblanco [1], Anna Westerbergh [1]

[1] *Swedish University of Agricultural Sciences, Department of Plant Biology and Forest Genetics, Box 7080, SE-750 07, Uppsala, Sweden*

Anna.Westerbergh@vbsg.slu.se

Cassava (*Manihot esculenta* spp. *esculenta*) is a tropical crop and produces starch-containing tuberous roots of world-wide importance as food. It is mainly vegetatively propagated through stem cuttings. It originates from South America and has been domesticated for more than 5000 years from its wild ancestor *Manihot esculenta* spp. *flabellifolia*. Selection during domestication has resulted in morphological and biochemical differences such as increased size of tuberous roots with higher starch content and thicker stems with enlarged meristematic zones (nodes) enabling vegetative propagation in cassava. Other traits were lost during the domestication of cassava such as resistance to pests and diseases and high protein root content and are only preserved in the wild relatives. Understanding which genetic changes and genes are involved in the evolution of new forms and traits are fundamental challenges in evolutionary biology. The main goal of this project is to study the genetic and phenotypic changes that have occurred during cassava domestication, especially to identify the genes that control trait differences between cassava and its wild ancestor and the relative magnitude of the effect of individual genes using a quantitative trait loci (QTL) mapping approach. An F_2 population derived from a cross between cassava and its wild ancestor is used to develop the first linkage map between cassava and a wild relative and to investigate the genetic basis of the evolution of cassava.

18-01 Poster

THE DOMESTICATION OF EUROPE

Terry Brown [1]

[1] *University of Manchester, Manchester Interdisciplinary Biocentre, M1 7DN, 131 Princess Street, UK, Manchester*

terry.brown@manchester.ac.uk

The objective of this project is to determine the extent to which phylogeographical analysis of modern landraces of barley and wheat can reveal genetic information pertaining to the spread and establishment of cereal cultivation from its points of origin in Southwest Asia into and through Europe. The approach is multidisciplinary, combining crop genetics with archaeobotany and archaeology. We have assembled a genetic database for extant landraces of barley and emmer, including both neutral loci and ones linked to adaptive traits, and we are attempting to give time depth to the genetic data by typing ancient DNA in archaeological and historic specimens. We are examining the genetic data to determine the extent to which its phylogeographical structure can be related to the trajectories by which agriculture spread through Europe during the Neolithic. Our expectation is that the ancient phylogeography will have been disguised by subsequent periods of crop movement and gene flow, but initial results suggest that the patterns of modern genetic variation preserve part of the Neolithic signature. This appears to be true both for Europe as whole, where the Mediterranean and central European trajectories of spread are still discernable in the genetic data, and in Italy, where phylogeographical analysis of microsatellite data reveals a point of origin that corresponds with the location of the earliest agricultural sites. Through study of adaptive trait genes such as the photoperiod response locus we have shown that the dispersal of barley to northern Europe was associated with adaptive evolution that enabled the plants to better utilise the novel climatic conditions to which they became exposed. Adaptive evolution might be linked to pauses that are thought to have occurred during the Neolithic agricultural spread across Europe.

18-02 Poster

WEEDS AND THE ORIGIN OF AGRICULTURE

Susan Thaw [1]

[1] *University of Manchester, Manchester Interdisciplinary Biocentre, UK, Manchester, 131 Princess Street, M1 7DN*

terry.brown@manchester.ac.uk

Lolium temulentum is a mimic weed associated with wheat and barley. Its distribution coincides with that of associated crops and the proposed origin of the genus Lolium lies between SW Asia and the Mediterranean Basin. Lolium temulentum originated when cereal cultivation began and its site of origin must therefore be close to the sites of wheat and barley domestication. In this study we are using the phylogenetic structure of Lolium temulentum to investigate the spread of agriculture. The basis for this is that it is believed that weeds will have undergone little or no artificial selection and hence the migration routes may be a good reflection of the different geographic routes that agriculture has taken. Previous studies using Lolium temulentum have detected intraspecific polymorphism among accessions from geographically separate regions using both microstatellites and ITS (internal transcribed spacer) sequences. In this study we have examined 76 accessions from across the distribution range and have utilised five microsatellites and the ITS region to investigate genetic diversity in this species in order to elucidate its phylogenetic history. The results presented here will be compared to data obtained by other projects we have been involved in on various wheats and barley.

18-03 Poster

USING ANCIENT DNA TO STUDY THE SPREAD OF AGRICULTURE IN SOUTH AMERICA

Terry Brown [1]

[1] *University of Manchester, Manchester Interdisciplinary Biocentre, 131 Princess Street, M1 7DN, Manchester, UK*

terry.brown@manchester.ac.uk

Desiccated plant remains often display excellent preservation of biomolecules, enabling DNA sequences to be obtained with good success rates from material up to 2000 years in age. This means that, when such material is available, ancient DNA can answer questions relating to the biogeography of cultivated plants. For example, through use of cobs obtained from cave sites, it has been possible to study the origins of South American maize, without the complicating factors introduced by the movement of genotypes during the post-Columbian period. This work has led to a model in which the two Central American agricultural systems – highland and lowland – generated separate expansions of maize cultivation into South America. One expansion centered on a highland culture that spread through the Panama highlands into the Andean regions on the west of South America, and the second expansion centered on a lowland culture which spread along the lowlands of the northeast coast of South America, entering the continent through the river systems. Maize specimens from Andean sites in northwest Argentina, dating from 400 to 1400 years before present, showed very little genetic polymorphism and were very similar to modern races of the Andean Complex, suggesting that this gene pool has predominated in the western regions of southern South America for at least the past 1400 years.

18-04 Poster

PHYLOGEOGRAPHICAL ANALYSIS OF WHEAT LANDRACES REVEALS THE POINT OF ORIGIN OF ITALIAN AGRICULTURE

Keri Brown [1], Andrew Isaac [1], Mark Muldoon [2], Terry Brown [1]

[1] *University of Manchester, Manchester Interdisciplinary Biocentre, UK, Manchester, 131 Princess Street, M1 7DN*
[2] *University of Manchester, School of Mathematics, UK, Manchester, Oxford Road, M13 9PL*

keri.brown@manchester.ac.uk

We typed five microsatellite loci in 52 accessions of Italian emmer wheat to determine if genetic analysis of wheats can provide information relevant to the spread of agriculture. Each of the five loci was polymorphic with 43 allele combinations identified in the 52 accessions. The allele combinations fell into two groups. Group 1 comprised 27 genotypes found in 42 accessions and Group 2 comprised 15 genotypes found in 10 accessions. The accessions with Group 1 allele combinations showed a strong correlation between geographical and genetic distances but those with Group 2 allele combinations did not . We inferred that the Group 1 accessions might therefore retain a phylogeographical structure that reflects ancient events. We present a phylogeographical model for the spread of agriculture which enables the point-of-origin of crop cultivation to be predicted by comparison between the genetic and geographical distances between accessions. We applied this model to the Group 1 accessions by positioning 131 hypothetical points-of-origin around the coastline and northern border of Italy. The highest correlation coefficients between genetic and geographical distances were seen for hypothetical points-of-origin located on the coast of northern Puglia. We repeated the analysis with 1040 hypothetical points-of-origin located within the Italian peninsula. Again, the highest correlation coefficients were located in northern Puglia. These predicted points-of-origin correspond with the location of the earliest agricultural sites in Italy. The results show that plant genetics can be used to study the spread of agriculture.

18-05 Poster

LOCAL-SCALE DIVERSITY DYNAMICS OF CASSAVA: A CASE STUDY OF TRADITIONAL FARMING SYSTEMS IN GABON, CENTRAL AFRICA

Marc Delêtre [1], Trevor Hodkinson [1], Doyle McKey [2]

[1] *Trinity College, Dublin, Botany Department, School of Natural Sciences, Trinity College, Dublin 2, Dublin, Ireland*
[2] *CNRS, Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), CNRS, UMR 5175, 1919 route de Mende, 34293 Montpellier Cedex 5, France*

deletrem@tcd.ie

Five hundred years after its introduction in the Old World, cassava (Manihot esculenta Crantz, Euphorbiaceae) in Africa is characterized by considerable genetic diversity, whose origin is not clearly understood. Genetic studies have demonstrated that African and neotropical cassava pools have comparable levels of diversity, suggesting that despite founder effects and the drastic reduction of diversity probably caused by the cassava mosaic disease pandemic, losses of diversity must have been balanced by processes of restoration of this diversity.

Five centuries of 'cultural' domestication have shaped the patterns of diversity of cassava in Africa, but whereas a number of reviews have stressed the extent to which African farmers, while adapting their farming systems or inventing new ones, have developed their own experience of cassava cultivation, nothing appears to be known about the 'roots' of this cultural domestication and their consequences for the diversity of the crop in its area of introduction.

Using a combination of ethnobiological surveys and population genetics, we undertook studies of traditional cassava farming systems in Gabon, central Africa, to investigate how cassava diversity originated. Our results support African cassava genetic diversity evolves as a metapopulation, with sources and sinks that had been determined by the historical context of the crop's introduction and diffusion into the Old World.

18-06 Poster

THE ORIGIN OF A, B AND G TRITICUM GENOMES BASED ON MOLECULAR DATA

Kseniya A. Golovnina [1], Sergey A. Glushkov [1], Nikolay P. Goncharov [1], Alexander G. Blinov [1]

[1] *Institute of Cytology and Genetics, Department of Molecular Evolution, Lavrent'eva street 10, 630090, Novosibirsk, Russia*

ksu@bionet.nsc.ru

The origin of four wheat genomes (A, B, D and G) whose various combinations form three groups of *Triticum* species on their ploidy (di-, tetra- and hexaploids) was a matter of discussion since more than seven decades. The correspondence of earlier evolutionary specifications to the phylogeny within the genus *Triticum* species has been estimated in present study. The relationships have been established based on chloroplast and nuclear DNA sequence data. It has been shown that *Ae. speltoides* was a donor of the plasmon for all polyploid wheat species, whereas the chloroplast genomes of the diploid *Triticum* species are close to other *Aegilops* species. Based on the obtained data the origin of the B and G genomes (Emmer and Timopheevii groups) was supposed as a result of two independent hybridization events within two ancestor forms of *Ae. speltoides* and diploid wheat. Nuclear *Acc-1* and *Pgk-1* genes have been used as the molecular markers for the A and B genomes of the *Triticum* species. No variability has been found in these genes within polyploid wheat genomes in spite of observed genome-specific differences. In contrast, three variants of these genes have been detected in the A genome of diploid *Triticum*. The detailed analysis showed that one of these variants (*T. urartu*) was a progenitor for all A genomes of all polyploid *Triticum* species; the second is close to *Ae. speltoides* genome; and the third is unique for wild diploid wheats. The further comparative-genetic analyses is necessary to resolve the relationships within diploid species.

18-07 Poster

THE SPREAD OF THE NEOLITHIC INTO EUROPE AS REVEALED BY ANCIENT PIG DNA

Greger Larson [1]

[1] *Uppsala University, Medical Biochemistry and Microbiology, BMC, Box 597, 751 24, Uppsala, Sweden*

greger.larson@imbim.uu.se

The Neolithic Revolution began 11,000 years ago in the Near East and preceded a westward migration into Europe of distinctive cultural groups and their agricultural economies, including domesticated animals and plants. Despite decades of research, no consensus has yet emerged regarding either the extent of admixture between the indigenous and exotic populations, or the degree to which the appearance of specific components of the "Neolithic cultural package" in Europe reflects truly independent development. Here, through the use of mitochondrial DNA from 323 modern and 221 ancient pig specimens sampled across western Eurasia, we demonstrate that domestic pigs of Near Eastern ancestry were definitely introduced into Europe during the Neolithic reaching the Paris Basin by at least the early 4th millennium BC. The appearance of unique pig haplotypes along two geographically isolated routes mirrors previous findings of domestic plant remains and indicates that incoming Near Eastern populations entered Europe along at least two separate routes: a northern Danubian Route that extended through the interior on the continent, and a southern Mediterranean Route which may have followed the coast line. Local European wild boar were also domesticated, possibly as a direct consequence of the introduction of Near Eastern domestic pigs. Once domesticated, European pigs rapidly replaced first the introduced domestic pigs of Near Eastern origin throughout Europe, and then, by the late Iron Age, they replaced native Near Eastern domestic stocks in Armenia. This large-scale spatial and temporal genetic analysis of a key component of the Neolithic Revolution reveals yet more complexity in the processes and interactions involving the spread of early farmers into Europe.

18-08 Poster

GEOGRAPHIC STRUCTURE IN GENETIC DIVERSITY OF T. DICOCCUM LANDRACES FROM ASTURIAS, SPAIN

Fiona Leigh [1], Ian Mackay [1], Lydia Smith [1], Wayne Powell [1]

[1] *NIAB, Diversity Genomics Group, Huntingdon Road, Cambridge CB3 0LE, UK*

fiona.leigh@niab.com

Emmer wheat, *Triticum dicoccum* was one of the founder crops of Neolithic agriculture. Though its cultivation was largely replaced by hexaploid wheats 2000 years ago, pockets of small scale cultivation remain. One such area is the Asturias region of Northern Spain, where emmer wheat remains a traditional crop and farmers grow locally adapted landraces. In order to study the diversity of these landraces, we sampled emmer wheat from different regions of Asturias, and genotyped multiple plants from each village using nuclear and chloroplast microsatellites. A high level of variation was observed with markers from both genomes, including a novel chloroplast haplotype. A strong geographic structure was observed in the Asturian emmer wheats in both the chloroplast markers and the nuclear SSR data.

18-09 Poster

PHYLOGEOGRAPHIC ANALYSIS OF CEREAL LANDRACES AIDS IN UNDERSTANDING THE SPREAD OF AGRICULTURE ACROSS EUROPE

Diane L. Lister [1], Hugo R. Oliveira [2], Mim A. Bower [1], Martin K. Jones [2]

[1] *University of Cambridge, The McDonald Institute for Archaeological Research, Downing Street, CB2 3ER, Cambridge, United Kingdom*
[2] *University of Cambridge, Department of Archaeology, Downing Site, CB2 3DZ, Cambridge, United Kingdom*

dll1000@cam.ac.uk

The field of plant genetics has shown the potential to play a key role in our understanding of the domestication of crops and the subsequent spread and establishment of agriculture. The Domestication of Europe consortium project has been exploring the spread of agriculture across Europe by the genetic analysis of European landraces of tetraploid wheat species (emmer, durum and rivet; Triticum turgidum subspp.) and barley (Hordeum vulgare). Historical cereal landrace material that pre-dates industrial agriculture and modern plant breeding has been included to determine the extent of "overstamping" of ancient genetic patterns and to fill in geographical gaps where modern landraces are not available. Material has been collected from a number of sources across Europe, including herbarium collections, museums and historic buildings. Our analysis of this material has shown that "historic" DNA, in contrast to "ancient" DNA from archaeological specimens, is less fragmented and therefore more useful for analysis with a wider range of genetic markers. We present the results of the analysis of both chloroplast and nuclear markers in modern and historic cereal specimens. These markers include ones linked to ecological adaptation such as the Ppd-H1 photoperiod response gene in barley, that has shown genetic variation distributed along a latitudinal cline. The analysis of such markers will help us to elucidate the role of crop adaptation versus human assimilation of agricultural practices in the stop-go pattern of Neolithic agricultural spread observed in parts of Europe.

18-10 Poster

THE EFFECTS OF PLANTING DENSITY ON THE TREND OF GRAIN FILLING ;YIELD AND YIELD COMPONENT OF THREE CHICK PEA (CICER ARIETINUM L.)VARIETIES IN KERMANSHAH

Keyvan Shamsi [1], Hamid Mehrpanah Mehrpanah [1]

[1] *Islamic Azad University; Kermanshah Branch; Iran, Department of Agronomy, poBox 67155-1774, Baghe Nai street, 123321, Kermanshah, Iran*

shams2_k@yahoo.com

A field experiment was conducted to evaluate effects of planting density and variety on the trendof grain filling; yield and yield component of chick pea .The present research was conducted at experimental farm of mahydasht(Ker Manshah).The factorial experiment was designed based on complete randomized block desigen with four replication. In this experiment; the variety in three level(Jam;ILC-482 and 12-60-31) and the planting density in three level 19; 28 and 57 plant.m-2) were considered. The trend of grain filling; yield ;yield component and agronomic characteristics; as some biomass yield; harvest index; number of pods per plant; number of grain per plant; number of node per main stem; plant height;number of branch per plant;weight of 100 grain;distance between 1st pod to soil;distance between 1st branch to soil and phonological stages the chick pea varieties based on photo growing degree day(PHOTO GDD) Were calculated. The result achieved showed that the maximum speed of grain filling related to density of 28 plant.m-2 and ILC-482 variety. Grain yield; number of pods per plant; number of grain per plant;weight of 100 grain; plant height;distance between 1st pod to soil and distance between 1st branch to soil were significantly affected by variety and density but number of branch per plant was affected by density and number of node per main stem and harvest index were affected by variety. The maximum photo growing degree day Related to 12-60-31 variety and the maximum grain yield related to density of 28 Plant.m-2

Key words:chick pea .variety .planting density .grain filling .yield .yield component

18-11 Poster

TRACKING THE ORIGIN AND SPREAD OF FINGER MILLET INTO SOUTH ASIA

Sally A. Stansbie [1]

[1] *University of Warwick, Warwick HRI, Wellesbourne, CV35 9EF, Coventry*

S.Stansbie@warwick.ac.uk

The available archaeobotanical evidence suggests that the earliest agriculture in South India occurred in the 3rd millennium BC, and was based on plants domesticated in the region. It is further believed that following the initial domestication, crops from other areas were adopted into the agricultural system. A number of cereals including sorghum, cowpea and finger millet are thought to have followed similar sea routed from Africa to India, around the 2nd millennium BC, arriving in India on the South or South-West Coast, and subsequently establishing a secondary centre of diversity and distribution.

This research is aimed at determining the path of Finger millet (*Eleusine coracana* Subsp. *Coracana*) following its movement and introduction from Africa to India. Finger millet has been chosen as the crop of interest as upon domestication and movement the species differentiated into three races showing different ranges and distributions, the morphological variability of finger millet has segregated out into groups displaying definite eco-geographical areas.

A number of loci are to be studied for phylogenetic information including the teosinte branched 1 locus, which provides information regarding changes in tilling structure over the course of domestication. Initial results obtained from examining the TB1 locus within finger millet accessions support a single entry point of the species into India on the South-West coast.

18-12 Poster

ASSESSMENT OF SHEEP DOMESTICATION HISTORY BASED ON MITOCHONDRIAL DNA DIVERSITY OF CONTEMPORARY OLD WORLD SHEEP

Emma Finlay [1], Miika Tapio [2], Gerold Kierstein [2], Han Jianlin [2], Olivier Hanotte [2]

[1] *Trinity College, Department of Genetics, 2, Dublin, Ireland*
[2] *International Livestock Research Institute (ILRI), Animal Genetic Resources, P.O. Box 30709, 00100, Nairobi, Kenya*

m.tapio@cgiar.org

The domestication of animals and cultivation of crops was one of the most important developments in human history. Mitochondrial DNA (mtDNA) studies have suggested multiple origins and revealed geographic structuring in livestock species. Sheep, together with goats, were the first domesticated livestock. The present study examines Old World sheep mtDNA diversity by combining published sequence data with new data from Africa, China and Britain. Four previously identified haplotype groups (A, B, C and D) had multiple occurrences. Among nearly one and half thousand sequences, group B was clearly the most common and widely occurring one. The group was particularly frequent in Africa and Europe. Haplogroup A was the second most common one being most frequent type in East Asia. Group C was less frequent peaking to nearly one fifth frequency in Asia. Haplogroup D was present in four animals around Near East and in two sheep in Mongolia. Some sequences do not cluster into these four haplogroups. Time since expansion was evaluated separately for each continent and each of the three most common haplogroups (A, B and C). Population expansions in Eastern Asia and Africa appeared most recently. Partitioning of genetic diversity within- and among continents revealed that differentiation between continents is broadly similar to that observed in goat, but it is clearly weaker than in cattle. Sheep contain multiple lineages reflective of multiple domestications or introgressions but the different events all occurred within the Middle East, and differences in haplotype distribution between different areas reflect migration patterns rather than being suggestive of distinct domestications in separate continents. Strong response to selection by livestock can be partly explained by the range of wild populations domesticated.

Plastic and evolutionary responses to temperature

19

Thursday August 23 *Location*: Ekonomikum 3

Symposium 19: Plastic and evolutionary responses to temperature

ORGANIZERS: Jacintha Ellers, Vrije Universiteit, The Netherlands
Klaus Fischer, University of Bayreuth, Germany

9.45-10.15	**Volker Loeschcke** (invited) Thermal adaptation and environmental stress: from selection experiments to gene expression studies and field releases
10.15-10.45	**George W. Gilchrist** (invited) Developmental plasticity in thermal sensitivity: as clear as night and day
10.45-11.05	**Wolf Blanckenhorn** Latitudinal clines and thermal adaptation in the yellow dung fly
11.05-11.35	*Coffee*
11.35-11.55	**Jan Kammenga** Genetics of the temperature-size rule in Caenorhabditis elegans
11.55-12.15	**R. Craig Stillwell** Environmental effects on sexual size dimorphism of a seed-feeding beetle
12.15-12.35	**Barbara Feldmeyer** The evolution of TSD without sex-specific effects of temperature
12.35-12.55	**Elizabeth Lacey** Adaptive thermoregulation in plants! A comparative study of floral reflectance patterns in European populations of Plantago lanceolata.
12.55-14.00	*Lunch*

19-01 Talk

THERMAL ADAPTATION AND ENVIRONMENTAL STRESS: FROM SELECTION EXPERIMENTS TO GENE EXPRESSION STUDIES AND FIELD RELEASES

Volker Loeschcke [1], Jesper Sørensen [1], Torsten Kristensen [1], Oleg Bubliy [2], Fabian Norry [3]

[1] University of Aarhus, Dept. of Biology, Ecology & Genetics, Ny Munkegade, Buildg. 1540, DK-8000, Aarhus C, Denmark
[2] Russian Academy of Sciences, Vavilov Institute of General Genetics, Gubkin Street 3, Moscow 119991, Russia
[3] Universidad de Buenos Aires, Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, C-1428-EHA, Buenos Aires, Argentina

volker.loeschcke@biology.au.dk

We are studying adaptation to environmental stress and its evolutionary implications with particular emphasis on thermal adaptation and the heat shock response. To achieve our research goals, we study correlated responses in lines selected for resistance to various environmental stresses as heat, cold, starvation and desiccation as well as lines selected for increased lifespan, which often has been shown to be related to stress resistance traits. Results on the phenotypic level are related to results on the DNA level, studying gene regulation in the same stress selected lines using Affymetrix gene chips at different time points after being exposed to a heat or cold hardening treatment. To complement these expression studies and to assess the role of putative candidate genes we use knockout or mutant lines and do quantitative PCR. Further, we map quantitative trait loci (QTL) responsible for thermal stress resistance, study DNA sequence variation in candidate genes and the relation of candidate gene variation to variation in resistance traits in natural populations and selection lines. We also study the metabolic profile in the selection lines to see which metabolites are affected by selection for stress resistance. Finally, we use some of the same selection lines to study fitness in the wild using release-recapture experiments to bridge the gap between laboratory experiments and studies of thermal adaptation in the wild.

19-02 Talk

DEVELOPMENTAL PLASTICITY IN THERMAL SENSITIVITY: AS CLEAR AS NIGHT AND DAY

George W. Gilchrist [1], Timothy C. Huber [1]

[1] College of William & Mary, Department of Biology, Box 8975, 23187, Williamsburg, VA, USA

gwgilc@wm.edu

Plastic variation in thermal sensitivity in response to developmental temperature is a well-known phenomenon, however much less is known about the effects of photoperiod. Since short days (8L:16D) should be a reliable cue for cold temperatures and long days (16L:8D) a cue for warm temperatures, the adaptive prediction would be that short day flies increase their cold tolerance and decrease heat tolerance, whereas long day flies would do the reverse. We examine photoperiodically cued changes in heat and cold sensitivity in Drosophila subobscura, a non-diapausing semicosmopolitan fruit fly, and in Drosophila melanogaster, a cosmopolitan, diapausing species. For both species, we find broad agreement with these predictions, especially for changes in cold tolerance. We will discuss some possible mechanisms mediating these changes and the implications of these findings for populations in a warming world.

19-03 Talk

LATITUDINAL CLINES AND THERMAL ADAPTATION IN THE YELLOW DUNG FLY

Wolf U. Blanckenhorn [1], Marco Demont [1], Paul I. Ward [1]

[1] *University of Zurich, Zoological Museum, Winterthurerstrasse 190, CH-8057, Zurich, Switzerland*

wolfman@zoolmus.unizh.ch, wolf.blanckenhorn@zm.uzh.ch

Large-scale clinal variation in quantitative and molecular genetic traits is often linked to seasonal or thermal adaptation. The wide-spread yellow dung fly, Scathophaga stercoraria (Diptera: Scathophagidae) in Europe shows a Bergmann cline for body size and a converse Bergmann cline (i.e. countergradient variation) for development time. We present indirect evidence for the adaptive nature of these clinal patterns by showing that clinal population variation in quantitative traits (Qst) is much greater than corresponding variation in putatively neutral molecular markers (Fst). Moreover, a causal relationship between thermal adaptation in quantitative and molecular traits may exist, as thermal adaptation crucially depends on alterations in the genetic, biochemical and physiological pathways functionally mediating thermal tolerance of the organism. Indeed, preliminary evidence suggests that phosphoglucomutase (PGM), an enzyme central to the mobilization and storage of glycogen and flight energetics, is under thermal selection in the yellow dung fly. In vitro assays further indicate that alleles differ in metabolic efficiency, thus potentially mediating thermal tolerance. Ongoing work investigates whether the latitudinal clines found in Europe replicate in North America and Japan (where yellow dung flies also occur), making an adaptation more likely, and whether PGM is indeed thermally selected in this species.

19-04 Talk

GENETICS OF THE TEMPERATURE-SIZE RULE IN C. ELEGANS

Jan Kammenga [1], Agnieszka Doroszuk [2], Joost Riksen [2], Esther Hazendonk [3], Laurentiu Spiridon [4], Andrei-Jose Petrescu [4], Marcel Tijsterman [3], Ronald Plasterk [3], Jaap Bakker [2]

[1] *Wageningen University, Nematology, Binnenhaven 5, 6709PD, Wageningen, The Netherlands*
[2] *Wageningen University, Laboratory of Nematology, Binnenhaven 5, 6709PD, Wageningen, The Netherlands*
[3] *Hubrecht Laboratory, Netherlands Institute of Developmental Biology, Uppsalalaan 8, 3584CT, Utrecht, The Netherlands*
[4] *Institute of Biochemistry of the Romanian Academy, Bucharest, Romania*

Jan.Kammenga@wur.nl

Ectotherms rely for their body heat on surrounding temperatures. A key question in biology is why most ectotherms mature at a larger size at lower temperatures, a phenomenon known as the temperature–size rule. Since temperature affects virtually all processes in a living organism, current theories to explain this phenomenon are diverse and complex and assert often from opposing assumptions. Although widely studied, the molecular genetic control of the temperature–size rule is unknown. We found that the *Caenorhabditis elegans* wild-type N2 complied with the temperature–size rule, whereas wild-type CB4856 defied it. Using a candidate gene approach based on an N2 x CB4856 recombinant inbred panel in combination with mutant analysis, complementation, and transgenic studies, we show that a single nucleotide polymorphism in *tra-3* leads to mutation F96L in the encoded calpain-like protease. This mutation attenuates the ability of CB4856 to grow larger at low temperature. Homology modelling predicts that F96L reduces TRA-3 activity by destabilizing the DII-A domain. The data show that size adaptation of ectotherms to temperature changes may be less complex than previously thought because a subtle wild-type polymorphism modulates the temperature responsiveness of body size. These findings provide a novel step toward the molecular understanding of the temperature–size rule, which has puzzled biologists for decades.

19-05 Talk

ENVIRONMENTAL EFFECTS ON SEXUAL SIZE DIMORPHISM OF A SEED-FEEDING BEETLE

R. Craig Stillwell [1], Charles W. Fox [1]

[1] *University of Kentucky, Entomology, S225 Agricultural Science Center North, 40517, Lexington, Kentucky, USA*

rstil2@uky.edu

Sexual size dimorphism is widespread in animals but varies considerably among species and among populations within species. Much of this variation is assumed to be due to variance in selection on males versus females. However, environmental variables could affect the development of females and males differently, generating variation in dimorphism. Here we use a factorial experimental design to simultaneously examine the effects of rearing host and temperature on sexual dimorphism of the seed beetle, *Callosobruchus maculatus*. We found that the sexes differed in phenotypic plasticity of body size in response to rearing temperature but not rearing host, creating substantial temperature-induced variation in sexual dimorphism; females were larger than males at all temperatures, but the degree of this dimorphism was smallest at the lowest temperature. This change in dimorphism was due to a gender difference in the effect of temperature on growth rate and not due to sexual differences in plasticity of development time. Furthermore, the sex ratio (proportion males) decreased with decreasing temperature and became female-biased at the lowest temperature. This suggests that the temperature-induced change in dimorphism is potentially due to a change in non-random larval mortality of males vs. females. This most important implication of this study is that rearing temperature can generate considerable intraspecific variation in the degree of sexual size dimorphism, though most studies assume that dimorphism varies little within species. Future studies should focus on whether sexual differences in phenotypic plasticity of body size are a consequence of adaptive canalization of one sex against environmental variation in temperature or whether they simply reflect a consequence of non-adaptive developmental differences between males and females.

19-06 Talk

THE EVOLUTION OF TSD WITHOUT SEX-SPECIFIC EFFECTS OF TEMPERATURE

Barbara Feldmeyer [1], Leo W. Beukeboom [2], Franz J. Weissing [1], Ido Pen [1]

[1] *University Groningen, Theoretical Biology, Kerklaan 30, 9750AA, Haren, The Netherlands*
[2] *University Groningen, Evolutionary Genetics, Kerklaan 30, 9750AA, Haren, The Netherlands*

b.v.feldmeyer@rug.nl

Temperature dependent sex determination (TSD) is phylogenetically widespread and has evolved multiple times from genetic sex determination (GSD), but the causes for these transitions are still poorly understood. Several hypotheses have been proposed, the Charnov-Bull hypothesis (CBH) being by far the most influential. The CBH assumes a sex-specific effect of temperature on fitness and predicts that for a given temperature, the sex with the highest reproductive value will develop. However, empirical support for the CBH is scant. Other hypotheses for TSD have not gone far beyond the stage of verbal arguments. We present a model that does not assume sex-specific fitness effects of temperature, but relies on selection for biased sex ratios due to local mate competition and local resource competition. Specifically, we assume a deme-structured population with sex-specific dispersal and varying levels of between-patch and within-patch fluctuations in temperature. Sex is determined by the interaction between temperature and three gene loci. Initially, the population has GSD (XY or ZW) determined by one of the loci. A second locus determines sensitivity of sex determination to temperature and a third locus specifies a temperature threshold. Four possible outcomes were observed: (i) the initial GSD state was stable; (ii) a new type of GSD evolved at the second locus; (iii) TSD evolved; (iv) a mixture of GSD and TSD evolved. As expected from previous work, TSD evolved more easily when temperature fluctuations were small and when life span was long. Unexpectedly, the initial GSD system (XY or ZW) can have a strong effect on the final outcome. Our main conclusions are that TSD can evolve more easily than expected without the CBH assumption of sex-specific fitness effects of temperature, and that mixtures of TSD and GSD can have long term stability.

19-07 Talk

ADAPTIVE THERMOREGULATION IN PLANTS! A COMPARATIVE STUDY OF FLORAL REFLECTANCE PATTERNS IN EUROPEAN POPULATIONS OF PLANTAGO LANCEOLATA.

Elizabeth P. Lacey [1]

[1] *University of North Carolina - Greensboro, Biology, 312 Eberhart Building, 27402, Greensboro, USA*

eplacey@uncg.edu

Biologists generally view thermoregulation as an adaptive attribute of animals. Our research shows that thermoregulation also occurs in multiple plant species. Some Plantago species partially thermoregulate their reproduction through temperature-sensitive plasticity in floral reflectance. Flowers produced at cool ambient temperatures are less reflective and darker than flowers produced at warm ambient temperatures. Increased anthocyanin production darkens flowers at cool temperatures in P. lanceolata. Floral reflectance plasticity in the visible and near-infrared spectral regions is significantly correlated with alternative oxidase activity. With multiple experiments, we are testing the hypothesis that thermoregulating reproduction is adaptive in P. lanceolata because warming reproductive organs and embryonic offspring in cool, but not warm, ambient temperatures increases fitness. One experiment examines the geographic variation in floral reflectance in European populations of P. lanceolata. Offspring derived from 29 populations were cloned, grown, and induced to flower at cool and warm temperatures. Mean floral reflectance and plasticity in reflectance were measured. Data support the hypothesis' prediction that mean reflectance should be negatively correlated with latitude and altitude. Data partially support the prediction that reflectance plasticity should be greater in the middle of the species' range. Results are discussed in the context of abiotic factors that differ across latitudinal and altitudinal gradients. Results provide evidence for local adaptation in thermoregulatory capability.

19-01 Poster

POLYMORPHISM AND DIVERGENCE AT REGUCALCIN (RC): A PARALOG OF THE DROSOPHILA COLD ACCLIMATION GENE (DCA)

Carlos Arboleda-Bustos [1], Carmen Segarra [1]

[1] *Universitat de Barcelona, Departament de Genetica, 08028, Barcelona, Spain*

cearboleda@ub.edu

Genes involved in tolerance, acclimatization and response to cold are good candidates to have suffered adaptive changes. The Drosophila cold acclimation gene (Dca) is up-regulated by cold treatment and is located at 88D on the 3R chromosome arm of D. melanogaster. This gene shares high similarity at the nucleotide and the amino acid levels with the Regucalcin (RC) gene, suggesting that Dca and RC have originated after a duplication event. RC maps on the X chromosome at 11A. In order to analyze the evolutionary forces shaping nucleotide variation at RC, patterns of intraspecific polymorphism and interspecific divergence have been analyzed. We sequenced a fragment of approximately 2.8 kb and 1.5 kb including the RC gene in D. melanogaster (13 lines) and D. subobscura (12 lines), respectively. Levels of silent polymorphism in D. melanogaster (pi = 0.009) are similar to those found in D. subobscura (pi = 0.006). No amino acid polymorphism was detected in any of the two species, indicating a strong purifying selection against nonsynonymous mutations. Divergence at the RC locus was estimated in five species of the melanogaster group and three species included in the obscura group. Divergence at nonsynonymous sites between the species of the melanogaster and obscura groups ranges from 0.06 to 0.12. A highly significant increase in the fixation rate of nonsynonymous substitutions was detected in the branch leading to D. subobscura, D. madeirensis and D. guanche.

19-02 Poster

ONTOGENETIC SHIFTS IN THE DIURNAL-NOCTURNAL FORAGING MODE IN RELATION TO PREDATION RISK AND TIME STRESS IN TERRESTRIAL INSECTS.

David Berger [1], Karl Gotthard [1]

[1] *Stockholm University, Deparment of Zoology, Stockholms Universitet, 10691, Stockholm, Sweden*

david.berger@zoologi.su.se

At large sizes, prey organisms are more conspicuous to their enemies and if size does not offer protection from predator attacks, mortality risk will be high. Size-mediated detection risks should decrease in darkness, so the night might offer a safer foraging opportunity to large individuals. Ontogenetic shifts from diurnal to nocturnal foraging have been well studied in aquatic systems. Here we present evidence of such shifts in terrestrial insect larvae. In one experiment we exposed the larvae of one seasonal and one non-seasonal butterfly to different levels of time stress and measured size-increase during the light- and dark periods throughout larval development. The results show that diurnal foraging ceased at large size while nocturnal foraging remained constant or even increased at larger sizes. In the non-seasonal species, time stress had little effect on the foraging behaviour while in the seasonal species larvae mainly fed during night time but increased risky day time feeding when exposed to time stress. In more resent epxeriments the larval feeding rythms of other satyrine species have also been investigated. Although the obvious benefit of risk reduction, it seems likely that strict night feeding might not be beneficial since the cold temperatures experienced during night puts contraints on development, especially in seasonal populations. Therefore we have also measured the temperature dependence of growth in some of the species in order to calculate expected development times in the field using the strict night time feeding strategy. The results turn attention to the importance of considering ontogenetic feeding shifts during the 24 hour period when investigating mechanisms regulating growth trajectories and other life history characters in the larvae of ectotherms.

19-03 Poster

GENETIC CONSTRAINTS TO ALTITUDINAL RANGE EXPANSION IN A GRASSHOPPER

Daniel Berner [1]

[1] *McGill University, Dept. of Biology, 859 Sherbrooke St. W., H3A 2K6, Montreal, Canada*

daniel.berner@mail.mcgill.ca

A view received from quantitative genetics is that most traits in most organisms hold abundant genetic variation, which should allow adaptive differentiation. This view contrasts with the common observation that ecological conditions often impose clear limits to an organism's range. This seeming paradox can be resolved by simultaneously identifying the factors that challenge an organism ecologically, and by exploring possible constraints to solving these challenges, which might arise from the structure of (co)variation between traits. This interplay between ecology and genetics was addressed in 13 populations of the European grasshopper *Omocestus viridulus* sampled along an altitudinal gradient of 2000 m. Field work showed that increasing altitude coincides with increasing time constraints on the life cycle owing to a decline in thermal season length. The comparison of grasshopper ontogeny under controlled laboratory conditions revealed that the diapause stage, a key trait in seasonal timing, is invariant in the species, reflecting a genetic constraint shared with other members of the subfamily. Further, I found a decrease in embryonic and larval developmental time in populations from high altitude. This differentiation in ontogeny is likely achieved by a shift in critical weight thresholds, since intrinsic growth rate was highly conserved among populations. Seasonal adjustment of larval development thus caused body size to decline pleiotropically with altitude, leading to a tradeoff between age at maturity and fecundity. Interestingly, growth rate did vary substantially within populations. Hence, patterns of ontogeny within populations cannot be used to predict population differentiation. Even though I document some altitudinal differentiation in grasshopper ontogeny, I conclude that this organism's potential to adapt to high-elevation seasonality is strongly constrained genetically.

19-04 Poster

RESPONSES TO COLD AND PHYLOGENETIC STRUCTURE IN THE SUBTERRANEAN CRUSTACEAN NIPHARGUS RHENORHODANENSIS.

Céline Colson [1], Frédéric Hervant [1], Christophe J. Douady [1], David Renault [2], Janine Gibert [1]

[1] *Université Claude Bernard Lyon 1, UMR-CNRS 5023, Laboratoire d'Ecologie des Hydrosystèmes Fluviaux, 69622, Villeurbanne Cedex, France*
[2] *Université Rennes 1, UMR-CNRS 6553, 263 avenue du Général Leclerc, 35042, Rennes Cedex, France*

celine.colson@univ-lyon1.fr

Subterranean organisms live in an extreme ecosystem and share common features linked to this biotope (e.g. hypoxia and food shortage tolerance, adaptation to the darkness, long life cycle). Living in a thermally buffered biotope, hypogean organisms should exhibit stenothermal characteristics. Niphargus rhenorhodanensis is an aquatic subterranean crustacean which lives in karstic, porous, and fissured aquifers. Ecophysiological studies showed that one population of this species (Chalamont, France), survived exposures at low temperature (0°C) and exhibited eurythermal characteristics. Surprisingly, this population was able to maximize performance over a large temperature range, including temperatures never endured in its natural habitat. Moreover, phylogenetic analyses demonstrated that this morphologically defined species can be divided into 6 independent evolutionary units. The aim of this study was thus to investigate if cold tolerance and responses reported for one of the six evolutionary units could be observed in the other lineages as well. Several ecophysiological parameters (oxygen consumption, ventilatory and locomotory activities) and metabolic responses (trehalose, glycerol, amino acids concentrations) were measured on 7 populations. These measurements were performed on kept organisms at 11°C (i.e. biotope temperature) and 3°C. We also performed genetic analyses to corroborate N. rhenorhodanensis phylogenetic structure. We found that the 7 populations studied, displayed a cold hardiness and belonged to 3 different evolutionary units. A plausible explanation links this cold tolerance to historical heritage as all populations were covered by ice during the Riss and the Würm glaciations in Jura (France).

19-05 Poster

A TRANSCRIPTOMIC APPROACH TO STUDY SEASONAL TIMING CONTROL OF THE REPRODUCTIVE POLYPHENISM IN THE PEA APHID

Teresa Cortés [1], Denis Tagu [2], Jean-Christophe Simon [2], David Martínez-Torres [1]

[1] *Universitat de València, ICBiBE, Apartado de Correos 22085, 46071, València, Spain*
[2] *INRA Rennes, UMR 1099 BiO3P, Agrocampus, BP35327, 35653, Le Rheu Cedex, France*

teresa.cortes@uv.es

Aphids (Aphididae:Hemiptera) are plant-sucking insects which are capable of both sexual and asexual reproduction in response to environmental changes. In nature, the length of photoperiod but also temperature plays an important role in modulating the reproductive response of aphid populations. Under long photoperiod (spring and summer) aphids reproduce by parthenogenesis. Shortening of photoperiod at the beginning of autumn is the key factor that induces the switch to sexual reproduction. Males and sexual females are produced and after mating, over-wintering eggs are laid. The molecular basis governing the mode by which aphids reproduce are far from being understood. Our goal was to identify genes regulated by seasonal changes involved in the reproductive polyphenism in the model aphid *Acyrthosiphon pisum*. Using a suppression subtractive hybridization (SSH) approach, reciprocally subtracted cDNA libraries between aphids subjected to short (sex inducing) and long (non inducing) days were constructed. This was done for two aphid strains exhibiting differences in their precise response to photoperiod conditions, the main difference being the effect of the temperature in their response. After sequencing of 2,112 ESTs, we identified 225contigs corresponding to short day up-regulated and 104 contigs corresponding to short day down-regulated genes. BLAST searches allowed the putative identification of 288 (87%) of the contigs. Some genes were selected for validation of their differential expression through RT-Quantitative PCR. For some genes (e.g. some cuticular proteins), different results were obtained for the two aphid strains analysed which raises the possibility that these differences could be related with the different responses that these two strains produce when exposed to short photoperiod conditions

19-06 Poster

GEOGRAPHIC VARIATION IN PHENOTYPIC PLASTICITY AND GENETIC ADAPTATION TO TEMPERATURE IN THE AFROTROPICAL BUTTERFLY BICYCLUS ANYNANA

Maaike A. De Jong [1], Bas J. Zwaan [1], Paul M. Brakefield [1]

[1] *Institute of Biology Leiden (IBL), Evolutionary Biology, Kaiserstraat 63, 2311 GP, Leiden, the Netherlands*

m.a.de.jong@biology.leidenuniv.nl

The East African butterfly *Bicyclus anynana* shows striking seasonal plasticity for wing patterns and life history traits, which functions as an adaptation to contrasting wet-dry seasonal environments, and the associated changes in food availability, resting background and predation. Temperature is the single most important climatic variable determining *B. anynana* seasonal phenotype for our well-studied population from Malawi, where temperature is highly correlated with rainfall and thus a reliable indicator for the correct seasonal form. However, patterns of temperature-rainfall correlation vary strongly throughout the distribution of *B. anynana,* and different regions therefore pose different selection pressures on the species' plastic responses to temperature.

We explore the nature and extent of phenotypic plasticity and genetic adaptation to temperature by comparing two Malawian populations and a population from South Africa at three temperatures in a family design. This set-up allows for the quantification of the reaction norm of the relevant life history traits, as well as the quantification of broad sense genetic variation for the traits at the individual temperatures as well as for the reaction norm. The traits that are analysed at this level were, larval, pupal, and total developmental time, pupal weight, fat content, and wing pattern elements. Moreover, the following adult life history traits were measured at the population level: resting metabolic rate (RMR) and adult starvation resistance. We will present the results of the experiment, which has been carried out successfully.

19-07 Poster

THE COST OF MAKING THERMAL PHENOTYPES

Gerard Driessen [1], Jacintha Ellers [1]

[1] *Vrije Universiteit, Institute of Ecological Sciences, Dept of Animal Ecology, De Boelelaan 1085, 1081 HV, Amsterdam, Netherlands*

gerard.driessen@ecology.falw.vu.nl

Plastic responses can have important advantages to organisms and, not surprisingly, many traits indeed are plastic. However, not all traits are equally plastic and there is a lot of variation in the degree and kind of plasticity. One of the issues involved in the evolution of plasticity is the production cost of a phenotype. These are the costs in terms of energy and resources that are directly associated with the making of an inducible phenotype.

Here we present an experiment in which we studied the cost of temperature-induced phenotypic plasticity. When subjected to a change in environmental temperature many organisms develop isozyme variants with different kinetic properties to compensate for suboptimal enzyme activity and fatty acid *cis*-unsaturation to counter decreased membrane fluidity. Hence temperature changes induce the development of adaptive thermal phenotypes.

We studied the influence of different exposure frequencies to high and low temperatures on the juvenile growth rate and survival in eighteen inbred lines of the collembolan *Orchesella cincta*. We hypothesize that if there are significant costs involved in making a thermal phenotype, then growth and survival should be reduced in treatments with high frequency temperature fluctuations compared to ones with a low frequency temperature fluctuations. The results show that the cost is line-specific: some inbred lines showed a reduced growth rate when exposed to high frequency fluctuations, whereas in most lines no difference could be detected between high and low frequency treatments. In a few lines high frequency exposure even led to higher growth rates. We conclude that the influence of production costs of thermal phenotypes on the evolution of thermal plasticity in *O. cincta* depends on the genetic composition of the population, but that they do not form a general constraint.

19-08 Poster

TEMPERATURE-MEDIATED CHANGES IN BUTTERFLY FLIGHT DESIGN: PATTERNS IN TIME AND SPACE

Melanie Gibbs [1], Christer Wiklund [2], Hans Van Dyck [1]

[1] *Catholic University of Louvain (UCL), Behavioural Ecology & Conservation Group, Biodiversity Research Centre, Croix du Sud, 4, 1348, Louvain-la-Neuve, Belgium*
[2] *Stockholm University, Department of Zoology, 10691, Stockholm, Sweden*

melanie_ri_gibbs@yahoo.co.uk

Variation in butterfly flight morphology has attracted much attention in evolutionary studies addressing the effect of selection by altered resource distributions on mobility in time (e.g. time series of a fragmented population) or space (e.g. continuous *vs*. fragmented population). First, we make an overview of what kind of adaptive morphological changes different studies have found focusing on flight-related traits (like wing length, wing surface, wing loading, amongst others) to test whether there is any consistency. Next, we address the issue of adult phenotype development in our model system, i.e. the speckled wood butterfly (*Pararge aegeria*). In this species seasonal variation and landscape-related differences have been shown before. Here we provide baseline data on flight morphology of a Swedish woodland population that was not affected by habitat fragmentation or any obvious regional warming (during 1990-1999). This allows us to explore to what extent *P. aegeria* is able to buffer its morphology or, alternatively, to conform its flight design based on the climatic conditions of development. As different seasonal cohorts correspond to different developmental pathways, we analyse these morphological time series relative to developmental pathway. We discuss the functional significance of the differences and argue for the need to test directly the functional significance of flight morphology in different behavioural contexts, rather than making vague assumptions as is often done in the literature.

19-09 Poster

THE EVOLUTION OF THERMAL PERFORMANCE CURVES IN SEMIAQUATIC NEWTS: THERMAL SPECIALISTS ON LAND AND THERMAL GENERALISTS IN WATER?

Lumir Gvozdik [1], Raoul Van Damme [2]

[1] *Institute of Vertebrate Biology, AS CR, Department of Population Biology, Studenec122, 67502, Konesin, Czech Republic*
[2] *University of Antwerp, Department of Biology, Universiteitplein 1, 2610, Wilrijk, Belgium*

gvozdik@brno.cas.cz

One of the most pervasive trends seen in nature is specialization and generalization. In semiaquatic ectotherms the convergent trend in variation of thermal performance curves (TPCs) for maximal locomotor capacity leads to thermal specialization (narrower TPCs) on land and thermal generalization (wider TPCs) in water. Because various functional, genetic, and selective associations prevent TPC parameters to vary independently on others, thermal specialization/generalization will evolve as a result of divergent patterns of covariation between TPC parameters in aquatic and terrestrial environment. Here we examine evolutionary patterns between parameters of TPCs for maximum swimming and running capacity within the lineage of European species of the newt genus *Triturus*. Phylogenetic comparative analyses reveal that running and swimming speed differ substantially in evolutionary patterns of variation and covariation between TPC parameters. However, the divergent thermal sensitivity of both speeds is not common for all species. Instead of thermal specialization/generalization, disparate thermal properties on land and in water lead to radically different evolutionary patterns in TPC variation: Whereas TPCs for swimming speed evolve mainly in shape (specialist-generalist direction), the shift in mean performance across all temperatures (vertical direction) accounts for most interspecific variation in TPCs for running speed in our study system.

19-10 Poster

ENERGETICS OF AN ADAPTIVE HEAT STRESS RESPONSE IN DROSOPHILA MELANOGASTER

Luke A. Hoekstra [1]

[1] *College of William and Mary, Department of Biology, Box 8795, 23187-8795, Williamsburg, VA, United States*

lahoek@wm.edu

Thermal stress resistance in insects has received a great deal of attention due to their nearly universal need to cope with variation in temperature, but the relationship between metabolic rate and thermotolerance remains poorly understood. During times of stressful environmental conditions, homeostasis is compromised and energetic efficiency becomes increasingly important. Thermotolerance requires metabolically costly process. Adaptation to heat stress may involve reducing metabolic rate during the resource-limited conditions of thermal stress, thereby conserving resources to compensate stress resistant mechanisms. Alternatively, changes in metabolic rate with temperature may simply depend on the non-adaptive result of the thermodynamic effects of temperature on biochemical reaction rates.

This study combines the use artificial selection and respirometry techniques to adrress the central question: Is the modulation of metabolic rate part of an adaptive heat stress response? I will investigate this question by comparing CO2 production of individual Drosophila melanogaster from populations artificially selected for high and low thermotolerance. If there is an adaptive metabolic stress response, we might expect selection on thermotolerance to have produced correlated differences in metabolic rate. I will present a thermal profile of metabolic rate during heat stress, comparing the metabolic performance of flies from low and high thermotolerant populations across a range of temperatures. Understanding the relationship between metabolic rate and stress tolerance will allow us to determing the functional significance of metabolic performance and the energetic capacity of species to cope with rising global temperatures.

19-11 Poster

CAN SPECIES WITH TEMPERATURE-DEPENDENT SEX DETERMINATION SURVIVE GLOBAL WARMING?

HULIN Vincent [1], Virginie DELMAS [1], Marc GIRONDOT [2], Matthew H. GODFREY [3], Jean-Michel GUILLON [1]

[1] *Université Paris XI, Ecologie, Systématique et Evolution, Batiment 362, 91405, Orsay, France*
[2] *Muséum National d'Histoire Naturelle, Laboratoire des Reptiles et Amphibiens, 25 rue Cuvier, 75005, Paris, France*
[3] *North Carolina Wildlife Resources Commission, Sea Turtle Project, 1507 Ann St., NC28516, Beaufort, USA*

vincent.hulin@u-psud.fr

The response of embryos sexual differentiation to temperature in species with Temperature-dependent Sex Determination (TSD) is traditionally characterized by two parameters: the pivotal temperature (P), defined as the theoretical constant temperature of sex ratio parity (1:1), and the transitional range of temperature (TRT), defined as the range of constant temperatures that yield both sexes. Inter-specific and even inter-population variations of these parameters with latitude have been proposed. Moreover, the sex ratio of individuals has been shown to have heritable components.

Most authors consider P alone as the best predictor of offspring sex and of the response of natural populations to temperature variations. We here show in our study that the proportion of nests producing both sexes (mixed nests) is positively correlated to the TRT in several TSD turtle species. These results were obtained using two complementary methods: (i) a statistical model based on published studies of natural populations and (ii) simulations with a new thermal model of TSD considering a mechanistic approach. We conclude that the value of TRT is of primary importance in predicting the consequences of global warming on TSD species.

Global warming is likely to result in increasingly female-biased populations in TSD turtle species. We predict that the probability for some individuals to produce males is higher in populations with a larger TRT. These individuals will get a selective advantage with increasing temperatures. Therefore, we predict that species with larger TRT are more likely to withstand global warming.

19-12 Poster

CLIMATE CHANGE AND TEMPORAL VARIATION IN NESTING BIOLOGY OF NORTH AMERICAN TURTLES

Fredric J. Janzen [1], J. Whitfield Gibbons [2], Judith L. Greene [2], John B. Iverson [3], John K. Tucker [4]

[1] *Iowa State University, EEOB, 253 Bessey Hall, 50011, Ames Iowa, USA*
[2] *SREL, 29802, Aiken, South Carolina, USA*
[3] *Earlham College, Biology, 47374, Richmond, Indiana, USA*
[4] *Illinois Natural History Survey, 62012, Brighton, Illinois, USA*

fjanzen@iastate.edu

Altered phenology of reproductive events has been noted as a particularly key indicator of biotic response to contemporary climate change. However, most research has focused on a single population of a given taxon (oftentimes at the edge of its geographic range), yet meta-analyses use such data as a proxy for the entire species. Moreover, few sufficiently long-term studies of phenology in reptilian taxa have been published. We address the possibility of climate-altered reproductive phenology with long-term (>10 years) data on nesting behavior in multiple populations of each of four genera of North American turtles (*Kinosternon*, *Chelydra*, *Chrysemys*, and *Trachemys*). We find that initiation of the nesting season has advanced significantly only in populations at the northern edge of the geographic range of a species. Populations located farther south within the geographic range of a species exhibited less marked temporal changes in nesting behavior. Our results appear to provide one explanation for the outcomes of meta-analyses that purport to exemplify the biotic impacts of climate change. We are now exploring what climatological variables explain the nesting patterns we observe in these turtles as well as testing whether the significant temporal shifts in phenology in populations at the northern edge of the range reflect phenotypic plasticity or adaptive evolutionary changes.

19-13 Poster

HSP70 AND HSP83 ARE NOT ASSOCIATED WITH ADULT THERMOTOLERANCE IN A NATURAL POPULATION OF DROSOPHILA MELANOGASTER

Louise T. Jensen [1], Torsten N. Kristensen [1], Volker Loeschcke [1], Ary A. Hoffmann [2]

[1] *Aarhus University, Ecology and Genetics, Ny Munkegade Build. 1540, Aarhus, Denmark*
[2] *Melbourne University, CESAR, 30 Flemington Road, Parkville Vic, Australia*

louise.t.jensen@nf.au.dk

Heat shock proteins (Hsps) are thought to be key proteins involved in the development of resistance to extreme temperatures and other stressors in organisms. However, studies in Drosophila are largely restricted to Hsp70, and to our knowledge, there are no prior studies on intra specific Hsp83 variation in Drosophila and its correlation to heat resistance or fitness traits. Hsp70 has been associated with survival to high temperature stress but negatively correlated with larval survival to adulthood, reflecting a trade-off between advantages and costs associated with this Hsp.

We have measured heat induced Hsp70 protein level as well as Hsp83 mRNA level in adults from 20 isofemale lines of D. melanogaster, collected from a central population on the Australian east coast. Adult heat resistance was measured using mortality and knock down assays. Additionally, we estimated fitness components such as egg to adult survival, developmental time and female fecundity.

Both Hsp83 and Hsp70 varied significantly among the isofemale lines investigated. Surprisingly, however, we found that expression levels of neither of the chaperones were associated with heat tolerance in adult flies. Furthermore, we did not observe trade-offs between Hsp70/Hsp83 and fitness. A large number of studies show that Hsps are important for coping with heat and both Hsps investigated in this study were clearly up-regulated in response to heat exposure. However since we were not able to detect correlated responses between expression and resistance levels among isofemale lines the association between the heat shock response and heat resistance is complex and variation in Hsp expression levels only seem to explain a small portion of variation in heat resistance.

19-14 Poster

ADAPTATION TO CHRONIC NUTRITIONAL STRESS IN DROSOPHILA MELANOGASTER AND ITS CONSEQUENCES FOR FITNESS-RELATED TRAITS

Munjong Kolss [1], Geraldine Schwaller [1], Tadeusz J. Kawecki [1]

[1] *University of Fribourg, Department of Biology, Chemin du Musee 10, 1700, Fribourg, Switzerland*

munjong.kolss@unifr.ch

Nutritional stress is commonly encountered by most species. Thus, the ability to cope with limited food is an important evolutionary adaptation. Many experimental studies have addressed the physiological responses to nutritional stress, in particular dietary restriction (DR). In a broad range of species, DR leads to reduced metabolism, higher resistance to oxidative stress, and increased life span, usually at the expense of decreased reproduction. In contrast to these physiological responses, which occur within the lifetime of an individual, much less is known about how exposure to chronic nutritional stress affects the evolution of populations over many generations. We addressed this issue, using an experimental evolution approach: replicate populations of *Drosophila melanogaster* were selected for high tolerance to chronic larval malnutrition. Within less than 20 generations, they outperformed unselected control lines by both surviving better and developing faster. Here, we report on the consequences of this evolution of increased tolerance to nutritional stress for adult fitness-related traits, including longevity, fecundity, and resistance to different stressors.

19-15 Poster

THE INFLUENCE OF EARLY ENVIRONMENT ON DEVELOPMENTAL PROCESSES AND LONG-TERM CONSEQUENCES FOR LIFE HISTORY

Alexander Kotrschal [1], Barbara Taborsky [2]

[1] *University of Bern, Behavioral Ecology, Wohlenstrasse 50a, 3032, Hinterkappelen, Switzerland*
[2] *International Institute for Applied System Analysis (IIASA), Evolution and Ecology Program, Schlossplatz 1, 2361, Laxenburg, Austria*

kotrschal@esh.unibe.ch

Certain life history traits may be determined irreversibly by the environment animals are exposed to during early life. In a previous study we showed that reproductive rate and offspring size of the African mouth brooding cichlid *Simochromis pleurospilus* are shaped by the environment encountered as juveniles, but remain fixed when the environment changes later in life. In this study we aim to identify (i) the proximate mechanisms leading to early canalization in certain life history traits, (ii) the developmental stage when fixation occurs and (iii) which developmental trade-offs are affected when phenotypes specialize on high or low reproductive investment early in life. We raised 140 young either in poor or rich nutritional environments and switched sub-groups of these fish to the opposite feeding regime at different stages during the juvenile period. We conducted repeated measurements on (i) growth, (ii) the allocation of energy to different body functions, (iii) physiological processes like assimilation efficiencies and SMR, and (iv) cognitive performance. Here we present the first results of this study and discuss the possible implications of the identified developmental trade-offs for the survival chances to adulthood and for reproductive schedules of adults.

19-16 Poster

TEMPERATURE-SIZE RULE IN ECTOTHERMS. CAN EXPLANATION BE SO SIMPLY?

Jan Kozlowski [1], Marcin Czarnoleski [1]

[1] *Jagiellonian University, Institute of Environmental Sciences, Gronostajowa 7, 30-387, Krakow, Poland*

kozlo@eko.uj.edu.pl

Temperature-size rule states that ectotherms usually grow slower in cold, but attain larger final size due to postponed maturation and prolonged growth period. Such response to temperature is observed in laboratory-reared animals and often lays behind geographical clines in body size. One possible proximate mechanism involved in dwarfing at higher temperatures is an inverse relation between temperature and cell size. However, if this relation was purely mechanistic, we could expect evolution of mechanisms compensating for fitness losses associated with the reduction of body size following development of smaller cell size (e.g., an increase of cell number). It seems more likely that having larger cells in cold is adaptive, and so important for fitness that a proper response of cell size to temperature is embedded in developmental program. We model this phenomenon based on the assumptions that: (i) maintenance of small cells is more costly because of necessity to maintain ion gradients on relatively larger surfaces; (ii) larger membrane surface permits more intense transport of supplies into a cell; (iii) the rate of biosynthesis is temperature-dependent and proportional to cell volume; and thus (iv) biosynthesis is demand-dependent in the cold and supply-dependent in the warm. Our mathematical model predicts that the optimal size of cells maximising rate of biosynthesis decreases with temperature if transport through membranes is strongly suppressed by cold than the rate of biosynthetic reactions inside cells. This precondition is testable, but we still do not know if it holds. Finally, we propose the way in which our cellular model can be integrated with existing models of temperature-driven evolution of life histories in ectotherms.

19-17 Poster

PARAMECIUM CAUDATUM: TEMPERATURE REACTION NORMS OF GENETICALLY CHARACTERIZED NATURAL ISOLATES.

Sascha Krenek [1], Dana Barth [1], Martin Schlegel [1], Thomas U. Berendonk [1]

[1] *University of Leipzig, Molecular evolution and animal systematics, Talstr. 33, 04103, Leipzig, Germany*

krenek@rz.uni-leipzig.de

Temperature is one of the most important environmental factors determining the reaction norms of small aquatic organisms like protozoa, because their body-temperature equilibrates quickly with the environmental temperature. Within the framework of global warming, studies on protozoa that focus on the ecological adaptation are of special interest to investigate the ecological consequences of elevated temperatures.

In this study, we have isolated several *Paramecium caudatum* cells from numerous freshwater habitats of different latitudes throughout Europe, correlating to different temperature zones. To examine their genetic background and their ecophysiology we have molecularly characterized these clones using the mitochondrial cytochrom *c* oxidase I (COI) gene and performed temperature dependent growth experiments to investigate their temperature reaction norms. Our data show that in *P. caudatum* exists no correlation between genetic and geographic distance. However, the investigated clonal lineages exhibit different temperature reaction norms, indicating the existence of various ecotypes in *P. caudatum* and suggesting a potential local adaptation, which correlates to the temperature regime of their native habitat.

19-18 Poster

ADAPTIVE DIFFERENCES IN GENE EXPRESSION IN EUROPEAN FLOUNDER (PLATICHTHYS FLESUS).

Peter F. Larsen [1, 2], Einar E. Nielsen [1], Timothy D. Williams [3], Jakob Hemmer-Hansen [1], James K. Chipman [3], Mogens Kruhøffer [4], Peter Grønkjær [5], Stephen G. George [6], Lars Dyrskjøt [4], Volker Loeschcke [2]

[1] *Technical University of Denmark, Danish Institute for Fisheries Research, Department of Inland Fisheries, Vejlsøvej 39, 8600, Silkeborg, Denmark*
[2] *University of Aarhus, Department of Ecology and Genetics, Ny Munkegade, 8000, Aarhus C, Denmark*
[3] *The University of Birmingham, School of Biosciences, B15 2TT, Birmingham, UK*
[4] *Aarhus University Hospital, Molecular Diagnostic Laboratory, 8200, Aarhus N, Denmark*
[5] *University of Aarhus, Department of Marine Ecology, Finlandsgade 14, 8200, Aarhus N, Denmark*
[6] *The University of Stirling, Institute of Aquaculture, FK9 4LA, Stirling, UK*

pfl@difres.dk

Until recently it was believed that population structure was very limited or absent in classical marine fishes due to extremely low levels of genetic subdivision measured using traditional DNA or protein markers. In recent years evidence of weakly differentiated local populations has been accumulating using non-coding markers, however, the evolutionary significance of such minute genetic differences remains largely unknown. To elucidate the relationship between genetic markers and adaptive divergence among populations of marine fishes we combined cDNA microarray, qRT-PCR and microsatellite analysis in European flounders (*Platichthys flesus*). Employing a long-term reciprocal transplantation setup mimicking natural salinities in the high-saline North Sea (33 ppt) and the brackish Baltic Sea (9 ppt) we demonstrate that a high number of genes were significantly differentially expressed between North Sea and Baltic Sea flounders despite extremely low levels of neutral genetic divergence (F_{ST}=0.006) between populations. Furthermore we present data pointing out the high importance of genetic background and relative low importance of environmental plasticity in respect to creating molecular gene expression phenotypes in flounders. Finally, several of the differentially regulated genes could be directly linked to fitness traits. These findings demonstrate that flounders, despite little neutral genetic divergence between populations, are differently adapted to local environmental conditions and imply that adaptation in gene expression could be common in other marine organisms with similar low levels of population subdivision.

19-19 Poster

HEAT RESISTANCE IN PARASITOIDS AND THEIR HOST

Cécile Le Lann [1], Olivier Roux [2], Joan Van Baaren [1]

[1] *Rennes1/UMR 6553 ECOBIO, Campus Beaulieu Bat 14 35042 Cedex Rennes, France, France*
[2] *UMR 5245 CNRS-UPS-INPT, Laboratoire d'Écologie Fonctionnelle, EcoLab (UMR 5245 CNRS-UPS-INPT), Université Paul Sabatier, Bât 4R3, 31062 Toulouse cedex 04, France., Toulouse, France*

cecile.lelann@univ-rennes1.fr

In Western of Europe, climatic changes results in an increase of mean temperature and a higher incidence of extreme weather like heat waves. For ectotherms, as insect parasitoids which develop inside or on an insect host killing it as a consequence of their development, high temperatures increase metabolic rate and may provoke physiological stress and reduce life span. Thus, differences in heat resistance may modify relations between parasitoids and hosts. In cereal crops in Brittany (France), three closely related *Aphidius* species of parasitoids (Hymenoptera: Aphidiinae) occur. *Aphidius rhopalosiphi,* which is the more abundant species and is present all year, *A. ervi* and *A. avenae,* which appear later and are less abundant, exploit the same host, the grain aphid *Sitobion avenae* (Hemiptera: Aphididae). We studied impact of heat stress by measuring locomotion disorders, immobility and temperature provoking death for both sex of each parasitoid species. We also measured aphid's immobility and temperature provoking death. Males of each parasitoid species always showed locomotion disorders and immobility at lower temperatures than females and all parasitoid species had lower immobility temperatures than their host. However, death temperatures differed between parasitoid sex and species and *A. rhopalosiphi* appeared to be less resistant to high temperatures than its host and the two other parasitoid species. There was high intraspecific variation in the heat resistance and parasitoid mass and length explained only part of this variance. We suggest that the remaining variance has a genetic basis. Is so, selection for increased heat resistance, especially in *A. rhopalosiphi* could result in adaptation to a warmer climate.

19-20 Poster

THE ROLE OF CLOCK AND OTHER CANDIDATE GENES IN THERMAL ADAPTATION IN EUROPEAN GRAYLING

Erica Leder [1], Thrond O. Haugen [2], Craig Primmer [1]

[1] *University of Turku, Biology, Vesilinnantie 5, 20014, Turku, Finland*
[2] *Norwegian institute for water research, Unit for Fish and Aquaculture, Gaustadalléen 21, N-0349, Oslo, Norway*

eriled@utu.fi

In plants and animals there is a set of genes collectively referred to as 'clock' genes that are responsible for maintaining circadian oscillations which in turn are entrained, or set, by environmental cues such as photoperiod and temperature. Temperature compensation of circadian components is especially important in ectothermic organisms such as fish, since they can experience large changes in core temperature and may need to adapt their physiology accordingly. European grayling in central Norway are of particular interest for studying the evolution of thermal adaptation in sympatric populations. Lesjaskogsvatnet is an elongated, shallow mountain lake oriented in an east-west direction. Due to the angle of incidence to the sun and other topological factors, streams entering into the lake experience large variations in flow and water temperature. In general, streams can be classified into either 'warm' or 'cold' relative to each other. Field observations indicate that fish spawning in 'warm' streams spawn up to three to four weeks earlier and their eggs experience higher temperatures during development than fish in 'cold' streams. Possible genetic mechanisms responsible for thermal adaptation to different streams are currently being examined in grayling with a particular focus on *clock* and other circadian genes. The *clock* gene is a good candidate as it was observed to be associated with a QTL for spawning time in rainbow trout, and it has a known role in the regulation of biological rhythms in other organisms. Sequences of the clock gene were obtained from grayling individuals from different spawning populations and examined for amino acid level changes. The significance of these sequence changes as well as expression levels of *clock* and other candidate genes for temperature-related differences in life history traits in grayling will be presented.

19-21 Poster

PREDATION AND TEMPERATURE: OPPOSING SELECTION PRESSURES ON INSECT COLORATION?

Carita Lindstedt [1], Leena Lindström [1], Mappes Johanna [1]

[1] *Jyväskylä, Bio- and Environmental Science, P.O. Box 35 University of Jyväskylä, FIN-40014, Jyväskylä, Finland*

carlind@cc.jyu.fi

Insect coloration is a result of several selection pressures among which predation and temperature are the most obvious ones. *Parasemia plantaginis* –moth larvae have phenotypically and genetically variable warning signal: orange patch on their otherwise black body. Thus, larvae with a small orange signal are darker i.e. more melanic compared to larvae with larger signals. We hypothesized that although predators learn to avoid large signalling larvae more effectively selecting for more conspicuous and large orange signal, thermoregulation might constrain the signal size in colder habitats. We predicted that melanic individuals should have significant advantage in cool climes if they can warm up more quickly and become active when non-melanics but more aposematic individuals cannot. We performed a full-sib rearing experiment with two selection lines (small and large orange signal) and with two temperature manipulations (high and low radiation environment). Temperature constrained the size and the brightness of the aposematic signal. Individuals developed smaller and darker signals in the low radiation treatment. The development time of the individuals from small signal selection line in the low radiation treatment was shorter than in the large signal selection line, suggesting that producing a large signal is costly in cold environments. This difference was consistent with the behavioural data. In the low radiation treatment the melanic larvae (small signal) spent more time on plant than less melanic larvae (large signal) indicating higher activity level of the melanic forms. Thus, temperature can cause environmental variation in the signal size supporting the idea that the cost:benefit ratio of the warning signals varies spatiotemporally.

19-22 Poster

SEASONAL FOOD INTAKE IN WILD AND GROWTH HORMONE-TRANSGENIC COHO SALMON AND THE ROLE OF THE GUT HORMONE CCK

Mare Lõhmus [1], Peter Raven [1], Fredrik L. Sundström [1], Robert H. Devlin [1]

[1] *DFO/UBC CAER, West Vancouver Laboratory, 4160 Marine Drive, V7V 1N6, West Vancouver/BC, Canada*

mare.lohmus@zool.gu.se

Seasonal variation in daily food intake is a well-documented phenomenon in many organisms. As an evolutionary adaptation to periods of low food supply, food intake in wild coho salmon (*Oncorhynchus kisutch)* is noticeably reduced during periods of decreased day length and low water temperature. Cholecystokinin (CCK) is a hormone involved in the regulation of daily foraging behaviour. The release of CCK mediates the feeling of satiety and has an inhibitory effect on food take. The objectives of this study were: first, to compare the seasonal changes in feeding behaviour between wild and growth hormone transgenic coho salmon with increased growth and appetite; second, to determine the behavioural effect of blocking the action of CCK (by using devazepide) on the seasonally adapted food intake; and third, to seasonally measure CCK expression in brain and gut tissues. We expected the food intake to be reduced in both types of salmon during winter, and hypothesizes that if CCK is a hormone involved in the regulation of seasonal foraging patterns, the largest response to the antagonist treatment (i.e. largest increase in food intake) is expected during the cold season. We also expected the expression of CCK in tissues to be increased during winter compared to the summer. We found that transgenic coho salmon, did not respond to the winter season with feeding reduction. Food intake was significant increase in both genotypes following the devazepide treatment in all seasons, but even if the increase in wild genotype was relatively higher during winter/spring than during summer, the treatment did not increase the appetite of the wild fish to summer levels. The expression of CCK in telencephalon differed significantly between winter and summer in wild salmon but not in the transgenics. Higher levels of CCK were detected in the gut of both genotypes whereas no differences in CCK expression were found in hypothalamus. It is therefore possible that CCK is an important mediator of seasonal food intake but its effect is largely influenced by other hormones.

19-23 Poster

TEMPERATURE AFFECTS WING DEVELOPMENT IN A FLIGHTLESS BEETLE MORPH

Suzanne T. E. Lommen [1], Suzanne V. Saenko [1], Kees G. Koops [1], Peter W. De Jong [2], Paul M. Brakefield [1]

[1] *Leiden University, Evolutionary Biology, Institute of Biology, Kaiserstraat 63, 2311GP, Leiden, The Netherlands*
[2] *Wageningen University, Laboratory of Entomology, P.O. Box 8031, 6700EH, Wageningen, The Netherlands*

S.T.E.Lommen@biology.leidenuniv.nl

Temperature does not only affect total body size, but can also affect specific body parts in different ways. Therefore, it can influence patterns of allometric growth. We will present a response of wing growth to temperature, using a flightless morph of the ladybird beetle *Adalia bipunctata*.

The morph displays a reduction in both pairs of wings (i.e. flight wings and elytra) and is under genetic control of a major locus. However, the phenotype varies widely in the degree of wing reduction, ranging from individuals completely devoid of wings to others only missing the extreme tips of their wings.

Firstly, we used two temperature regimes to show a plastic response in wing reduction. The strength of the response was family-dependent indicating a gene-by-environment interaction. We then explored this interaction in more detail by exposing flightless lines that had been artificially selected for large or small reduction in wings to the same temperature regimes. Secondly, we investigated the mechanisms causing variation in wing reduction by histological studies of larval wing development. We will show that variable wing phenotypes result from variation in wing growth rate.

19-24 Poster

RESPONSES TO TEMPERATURE SELECTION IN LEPTINOTARSA DECEMLINEATA AND THEIR EFFECTS ON PHYSIOLOGICAL AND LIFE-HISTORY TRAITS

Anne Lyytinen [1], Sanna Boman [1], Leena Lindström [1], Johanna Mappes [1], Saija Piiroinen [1]

[1] *University of Jyväskylä, Department of Biological and Environmental Science, P.O.Box 35, 40014, University of Jyväskylä, Finland*

alyytine@bytl.jyu.fi

The effects of the thermal evolution on physiological and life-history traits were studied using a selection line experiment. Parental generation of *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) was raised at two fluctuating temperatures (mean either 17°C or 23°C) for three generations and selected for faster development. Their offspring were raised either at constant 23°C or under one of the two fluctuating temperature regimes (mean 17°C or 23°C). At constant 23°C, parental temperature affected fat body content but not development times. The beetles whose parents had been raised at high fluctuating temperature had higher lipid content although they did not differ in adult weight. In the thermoperiod of mean 17°C, beetles whose parents had been raised under this temperature regime had a faster development time and a bigger body mass than beetles whose parental temperature had been high, fluctuating 23°C. When beetles were raised in the thermoperiod of mean 23°C, parental temperature influenced adult weight but not development times. Beetles whose parents had been selected under high temperature regime had a smaller body mass. Thus, we found the effects of parental temperature on offspring traits and evidence for thermal evolution under laboratory conditions but effects depend partly on temperature.

19-25 Poster

OVERWINTERING SELECTION IN DROSOPHILA MELANOGASTER, ASSOCIATIONS BETWEEN GENETIC MARKERS AND FIELD FITNESS

Nina Poulsen [1], Mark Blacket [2], Ary Hoffmann [2]

[1] *University of Aarhus, Ecology and genetics, Ny Munkegade building 1540, 8000, Aarhus, Denmark*
[2] *University of Melbourne, Center for environmental stress and adaptation research, 3010, Melbourne, Victoria, Australia*

nap@difres.dk

Drosophila melanogaster has been intensively studied along the latitudinal cline of the Australian east coast. The results of these studies have revealed strong clines in many phenotypic traits as well genetic markers. The steepness of the clines and existence of similar clines on different continents support that natural selection is the main driving evolutionary force. The identification of numerous traits and genes associated with climatic adaptation in a model species with a recent colonisation history provides a better understanding of how climatic adaptation occurs and may assist in predicting changes in species distributions under future climate change. In our study we investigated selection on a short-term scale by looking for associations between phenotypic traits and genetic markers under semi-natural conditions. *Drosophila melanogaster* flies originating from three populations along the east coast of Australia were all set up in field cages under Melbourne winter conditions and kept in these to the end of the winter. Phenotypic traits were measured and associated with eleven genetic markers, many candidate genes involved in stress response and cold adaptation. All phenotypic traits investigated showed interpopulation differences. By combining phenotypic traits with the results from genetic markers, we identified significant changes in genotypic composition over winter within populations showing short-term selection, but also a significant association between genetic markers and fecundity/fertility. To our knowledge this study is the first to document changes in genetic markers in relation to overwintering field fitness.

19-26 Poster

LARGER IN SPITE OF LOWER FOOD QUALITY AND HIGHER TIME CONSTRAINTS: COUNTERINTUITIVE SEASONAL BODY SIZE PATTERNS IN BIVOLTINE MOTHS

Tiit Teder [1], Triinu Mänd [2], Anu Sang [2], Toomas Tammaru [2]

[1] University of Tartu, Institute of Botany and Ecology, Lai 40, 51005, Tartu, Estonia
[2] University of Tartu, Institute of Zoology and Hydrobiology, Vanemuise 46, 51014, Tartu, Estonia

tiit.teder@ut.ee

In temperate areas, seasonality creates a universal time constraint on developmental schedules of insects. Whereas univoltine insects have to fit a single generation into the favourable season, bi- and multivoltine species have an additional adaptive challenge: splitting the season between two or more generations in an optimal way. Within the favourable season, different generations experience different combinations of time constraints, temperature, food resources and mortality risk. Consistently, the optima for development time and growth rate, and thus, for final body size, are not necessarily the same for different generations. A number of optimality models have been constructed to predict the response of between-generation size patterns to particular environmental factors. In contrast, empirical data showing the net effect of different factors on seasonal patterns of body size are surprisingly scarce.

We examined between-generation size differences in 12 temperate bivoltine moths. In most species, both males and females having developed late in the season appeared to attain larger adult sizes than conspecifics with the juvenile development early in the season. This pattern itself indicates that neither time limitation (greater in the end of the season) nor food quality (higher in the beginning of the season) can play a decisive role in determining seasonal patterns of body size in these species. A rearing experiment with one of these moths suggests that neither can this pattern be attributed to proximate influence of temperature. However, our field estimates of larval mortality suggest that seasonal differences in this variable may be solely responsible for the patterns observed: larvae developing in late summer can afford to grow larger due to lower activity of insectivorous birds.

19-27 Poster

EFFECTS OF TEMPERATURE ON BREEDING TIME IN A LONG LIVED BIRD POPULATION (RED-BILLED GULL)

Celine Teplitsky [1], Jim A. Mills [2], Juha Merilä [1]

[1] Helsinki University, Biological and environmental Sciences, Biocenter 3, Viikinkaari 1, 00014, Helsinki, Finland
[2] 10527a Skyline Drive, 14830, Corning, USA

Celine.Teplitsky@helsinki.fi

The abundant evidence for phenotypic responses to global warming has increased attention to responses to temperature. However, the relative roles of phenotypic plasticity and microevolution as mechanisms explaining these responses are largely unknown. Breeding time is a trait closely associated to fitness, and although it is known to be heritable, it is also highly sensitive to temperature. Accordingly, earlier breeding with increased temperature has been reported in many studies, but in the context of climate change, the role of phenotypic plasticity vs. microevolution in explaining those changes is still unclear. Quantitative genetics provides a framework to disentangle genetic from environmental influences in phenotypic expression. Comparing trends in breeding and phenotypic values gives precious information on the amount of plasticity involved in responses to an environmental variable. More recently, random regression models have allowed getting deeper insights in the quantitative genetics of plastic responses. In my presentation, I will investigate temperature effects, genetics and selection on breeding time in an exceptional data set from a wild red-billed gull population using more than 40 years of data on individually marked birds and pedigree information for more than 14000 individuals. Preliminary results indicate surprising and exciting advances as suggested by the greater heritability of laying date in males than in females.

19-28 Poster

FECUNDITY SELECTION PREDICTS BERGMANN'S RULE IN SYNGNATHID FISHES

Tony Wilson [1]

[1] *University of Zurich, Zoological Museum, Winterthurerstrasse 190, 8057, Zurich, Switzerland*

tony.wilson@zoolmus.unizh.ch

The study of latitudinal increases in organismal body size (Bergmann’s Rule) predates even Darwin’s evolutionary theory. While research has long concentrated on identifying general evolutionary explanations for this phenomenon, recent work suggests that diverse factors operating at local phylogenetic scales may be the cause of this widespread trend. Bergmann’s Rule explains body size variation in a diversity of warm-blooded organisms and there is increasing evidence that Bergmann’s Rule is also widespread in ectotherms. Bergmann’s Rule operates differentially in species of the Syngnathidae, a family of teleost fishes noted for extreme adaptations for male parental care. While variation in body size of polygamous *Syngnathus* pipefish is consistent with Bergmann’s Rule, body size is uncorrelated with latitude in monogamous *Hippocampus* seahorses. Study of populations of *Syngnathus leptorhynchus* along a natural latitudinal and thermal gradient indicates that increases in body size with latitude maintain the potential reproductive rate of males and that multiple mating is necessary in order to maximize male reproductive success, supporting a link between fecundity selection and Bergmann’s rule in brooding species.

Mating competition and sex-role dynamics

20

Saturday August 25 *Location*: University building X

Symposium 20: Mating competition and sex-role dynamics

ORGANIZERS: Tony Wilson, University of Zürich, Switzerland
Ingrid Ahnesjö, Uppsala University, Sweden

9.45-10.15 **Stephen Shuster** (invited)
The operational sex ratio, the potential reproductive rate and the opportunity for sexual selection

10.15-10.45 **Lotta Kvarnemo** (invited)
Operational sex ratio and varying sexual selection

10.45-11.05 **Hanna Kokko**
Why do males compete for matings?

11.05-11.35 *Coffee*

11.35-11.55 **Stéphanie Bedhomme**
Sexual conflict and immune function: Is immunocompetence a sexually antagonistic trait?

11.55-12.15 **Katja Heubel**
Female-biased operational sex ratio increases the current reproductive effort of females
12.15-12.35 **Suzy Renn**
Sex, sex-roles, and dominance: a functional genomics approach

12.35-12.55 **Henrik Pärn**
Age before beauty - Do ornament fitness-correlations in female birds imply male mate choice?

12.55-14.00 *Lunch*

20-01 Talk

THE OPERATIONAL SEX RATIO, THE POTENTIAL REPRODUCTIVE RATE AND THE OPPORTUNITY FOR SEXUAL SELECTION.

Stephen M. Shuster [1]

[1] *Northern Arizona University, Biological Sciences, Bldg. 21 S. Beaver St., 86011, Flagstaff, USA*

stephen.shuster@nau.edu

Many researchers have attempted to quantify the intensity of sexual selection using estimates of a species' operational sex ratio (OSR), or of its potential reproductive rate (PRR). In general, these measures include only those individuals who are sexually receptive at a particular time and place, or whose maximum rate of reproduction can be experimentally manipulated. Here, I show that the practice of including certain individuals and excluding others in such procedures can cause errors in estimates of the sex difference in the variance in relative fitness; i.e., in the opportunity for sexual selection. I also show that, depending on the consistency of individual mating success within the breeding season, high and low values of OSR can lead to identical estimated intensities of mating competition. Lastly, I show how the contributions, of local variation in sex ratio, and the consistency of individual mating success, to the opportunity for sexual selection, can be specifically identified by partitioning the distribution of successful matings into spatial and temporal components. Because estimates of OSR and PRR can provide incomplete or erroneous information about sexual selection, and because the opportunity for sexual selection can be measured with considerable precision, I conclude that the opportunity for sexual selection is a more reliable estimator of sexual selection's intensity than either OSR or PRR.

20-02 Talk

OSR & VARYING SEXUAL SELECTION

Lotta Kvarnemo [1]

[1] *Göteborg University, Dept of Zoology, Dept of Zoology, Box 463 , Göteborg University, SE-40530, Göteborg, Sweden*

lotta.kvarnemo@zool.gu.se

The operational sex ratio (OSR) is a well established and widely used concept in studies on sexual selection. Even though its usefulness has recently been questioned, I do not think we should stop using OSR - but we need to be very clear on its strengths and its limitations: It is important to bear in mind 1) that OSR is not (and has never been) a measure of sexual selection, and 2) although OSR has proven itself to be a good predictor of mating competition, reflected in conventional or reversed sex roles, mating competition is only one of many sources of sexual selection. In my talk, I will focus on what I see as the real merits of OSR, namely how it can help us identify a range of other factors that all can contribute to the level of sexual selection in a population. Such factors include, for example, parental investment, adult sex ratio, age and size distribution in the population, abundance and size distribution of nest sites, food abundance, water temperature, reproductive life span of males and females, predation rate and migration patterns. By structuring how each factor may influence OSR, via the relative potential reproductive rates of the sexes, or via the adult or qualified sex ratio, we can reach a better understanding of how these factors may influence the level of mating competition in our study populations. Many of these factors vary substantially within and between populations, which may generate variation in mode, direction and intensity of sexual selection. This variation is interesting in itself, and, rather than trying to remove it, I encourage everyone to go out and actively look for it. In this work, you will find many different conceptual tools useful. My guess is that OSR will be one of them.

20-03 Talk

WHY DO MALES COMPETE FOR MATINGS?

Hanna Kokko [1], Michael D. Jennions [2]

[1] *University of Helsinki, Biological and Environmental Science, PO Box 65, 00014, Helsinki, Finland*
[2] *Australian National University, Botany & Zoology, Canberra, 0200, Canberra, Australia*

hanna.kokko@helsinki.fi

Our understanding of sex roles is based on anisogamy and the operational sex ratio: when there is a relative shortage of large female gametes compared to small male ones, males are the sex that has to invest more in competition over matings (instead of caring for current offspring). However, in cases where males are observed to be monogamous, the very same argument — a limited number of available females — has been used as an argument favouring staying with the current female and her offspring. Indeed, why should a male be so keen to participate in mating competition if it is difficult to succeed there, and one could more usefully care for current offspring? The field lacks a proper theoretical underpinning when the same argument is used to explain two exactly opposite outcomes. We will argue that attempts to answer the question "why does sexual selection act more strongly on males?" have suffered from not considering alternative options that individuals have (e.g. caring, mate-guarding), and our aim is to present models that give more comprehensive answers than have been available so far.

20-04 Talk

SEXUAL CONFLICT AND IMMUNE FUNCTION: IS IMMUNOCOMPETENCE A SEXUALLY ANTAGONISTIC TRAIT?

Stéphanie Bedhomme [1], Kurt A. McKean [2], Pan-Pan Jiang [1], Nagaraj G. Prasad [1], Adam K. Chippindale [1]

[1] *Queen's University, Biology, 116 Barrie Street, K7L3N6, Kingston, Canada*
[2] *Cornell University, Molecular Biology and Genetics, Biotechnology Building, NY 14853-2703, Ithaca, USA*

bedhomme@biology.queensu.ca

Intralocus sexual conflict can inhibit the evolution of each sex towards its own fitness optimum. Whereas evidence of intralocus conflict recently accumulated in a variety of organisms ranging from plants to mammals, its evolutionary implications and the specific traits involved in the conflict have been poorly investigated. We developed *Drosophila melanogaster* lines in which the transmission of the genome was limited to males for several dozen generations. These male-limited (ML) lines, freed from female selection pressures, showed markedly increased male fitness. When experimentally expressed in females, ML genomes caused a strong reduction in fitness. Evidence points to the masculinisation of various traits involved in development and reproductive behaviour. Here we report on the evolution of their immunocompetence. Immunocompetence is known to be a sexually dimorphic trait in *Drosophila* and other organisms, with females having a higher immunocompetence than males. However, the selection pressures shaping this dimorphism as well as the role of non-genetic factors such as diet or reproductive conditions are under debate. The male-limited lines, by their experimentally evolved nature, constituted ideal material to shed new light on this question. Our results suggest that males and females have different optimal immunocompetence levels and that these levels are affected by diet. They also suggest that the selection pressures shaping the dimorphism may be indirect, through correlations between immunocompetence and other important fitness traits such as reproductive behaviour and fecundity.

20-05 Talk

FEMALE-BIASED OSR INCREASES THE CURRENT REPRODUCTIVE EFFORT OF FEMALES

Katja U. Heubel [1]

[1] *University of Helsinki, Department of Biological and Environmental Sciences, PO Box 65, FIN-00014, University of Helsinki, Finland*

katja.heubel@helsinki.fi

For females it is usually assumed that access to males does not limit their reproduction. However, this broad generalization often fails and female-female competition for access to male parental investment occurs. So far, little attention in this context has been paid to the female's reproductive effort. Life-history theory predicts that when prospects of future reproduction diminish, current reproductive effort should increase. One should expect increased early reproductive effort in response to strong competition for mates, whenever access to mates limits reproduction. Species that often experience fluctuations in the OSR can be expected to possess reaction norms that relate current reproductive effort immediately to the OSR. However, experimental evidence for such a response is lacking. Here the OSR in a pool experiment on common gobies (*Pomatoschistus microps*) was manipulated to study the interplay between OSR and reproductive rates and to test if females respond to a scarcity of males by increasing their early reproductive effort. Female reproduction in a female-competitive environment was characterized by larger clutches, faster reproduction, but fewer consecutive clutches. To our knowledge this experiment is the first demonstration that female fish adjust their life history strategy as a response to the current competitive setting.

20-06 Talk

SEX, SEX-ROLES, AND DOMINANCE: A FUNCTIONAL GENOMICS APPROACH

Suzy C. P. Renn [1], Hans Hofmann [2]

[1] *Reed College, Biology, 3203 SE Woodstock Blvd, 97202, Portland OR, USA*
[2] *University Texas, Austin*

suzy@reed.edu

I address the interactive role of the genome and the environment on behavioral phenotype by profiling gene expression in the brain of the African cichlid fishes. My initial work identifies the gene expression profile of socially regulated dominant and subordinate phenotypes using male Astatotilapia burtoni. This reversible switch includes both behavioral and physiological changes. I next take advantage of an experimental manipulation of female behavior in order to separate male-like reproductive behavior and male reproductive physiology. In the absence of males, females change their behavior and exhibit male-typical phenotypes without changing sex. These "territorial females" obtain male-like coloration, exhibit territoriality, boarder threats as well as male-like courtship and spawning behavior. I compare neural expression profiles of territorial and non-territorial females with those normally observed in the two male phenotypes thus controlling for the effects of sex and reproductive status. Interestingly, brain expression profiles of territorial females share a significant number of genes that are also identified as "male-typical" suggesting that these females are "masculinized". Even more striking is the finding that some genes are up-regulated in the brains of dominant fish, regardless of sex suggesting that there is in fact a "dominance module" of gene expression. In addition to the generation of gene lists for follow-up, I use bioinformatics approaches such as Gene Ontology (GO) terms in order to reduce experimenter bias in analysis. I aim to extend these studies to inter-species comparisons to examine the diversity of mating and brooding strategies that has arisen during the rapid and recent radiation if cichlid species.

20-07 Talk

AGE BEFORE BEAUTY - DO ORNAMENT FITNESS-CORRELATIONS IN FEMALE BIRDS IMPLY MALE MATE CHOICE?

Henrik Pärn [1], Frode Fossøy [1], Arild Johnsen [1], Jan T. Lifjeld [1]

[1] *University of Oslo, Natural History Museum, P. O. Box 1172 Blindern, 0318, Oslo, Norway*

henrik.parn@nhm.uio.no

Correlations between female ornamentation and reproductive success have commonly been interpreted as support for sexual selection on the female ornament. However, condition dependence of both the ornament and reproduction may create a correlation between the two, without sexual selection acting on females. In this study, we consider benefits and constraints of male choice for female ornaments in bluethroats *Luscinia svecica,* a migratory passerine. We show that ornament expression and reproductive success in female bluethroats are age-dependent traits, that older females arrive and breed earlier than younger females, and that more ornamented females do not have higher reproductive success when the seasonal decline in reproductive success is controlled for. Male bluethroats would therefore benefit from breeding with early-arriving females, regardless of their ornamentation. Hence, we argue that female ornamentation is not a trait selected for through male mate choice in bluethroats. The female ornament, and its condition dependence, have rather evolved as a correlated response to sexual selection on the ornament in males. Our findings have broad implications for the understanding of evolution of male mating preferences and female ornaments, especially in migratory birds. We emphasize the need to consider constraints on male choosiness and possible confounds to ornament-fitness correlations.

20-01 Poster

REPRODUCTIVE BEHAVIOUR AND PHYSIOLOGY OF MALE GREY-CHEEKED MANGABEYS IN KIBALE NATIONAL PARK, UGANDA

Malgorzata E. Arlet [1]

[1] *UC Davis, Entomology and Anthropology, One Shields Avenue, 95616, Davis, USA*

maarlet@yahoo.com

In many species, male reproductive tactics differ among individuals as a function of male social status. We observed reproductive tactics and male status, and measured cortisol and testosterone levels, and various health determinants from urine of adult male grey-cheeked mangabey (*Lophocebus albigena johnstoni*). High-ranking males had higher concentrations of testosterone than other males and were also more successful in obtaining matings. When females at the peak of sexual swelling were present in the group, male cortisol levels were elevated. Male involvement in fights was strongly correlated with his cortisol and testosterone concentrations. Migrating males showed higher levels of cortisol than resident males. Mating success, loud calls, consortships and aggression towards females and males were correlated with each other and related to male rank. Five studied groups differed significantly in cortisol and testosterone levels: the highest levels of cortisol and testosterone were observed in group with the highest number of males. This results show that in social animals, like mangabey, male mating tactics are costly, and can have health consequences.

20-02 Poster

EVIDENCE FOR INTRA-EJACULATE CRYPTIC FEMALE CHOICE IN SEAWEED FLIES (DIPTERA: COELOPIDAE)

Jennifer E. Blyth [1, 2], Andre S. Gilburn [3]

[1] *Åbo Akademi University, Environmental & Marine Biology, Akademigatan 1, FI 20500, Åbo/Turku, Finland*
[2] *University of Leicester, Department of Biology, Adrian Building, University Road, LE1 7RH, Leicester, UK*
[3] *University of Stirling, School of Biological and Environmental Sciences, Cottrell Building, FK9 4LA, Stirling, UK*

jennifer.blyth@abo.fi

The seaweed fly, *Coelopa frigida*, is an ideal model organism for studying cryptic female choice due to its extremely high natural re-mating frequency and the strong heterosis that operates on the basis of the αβ inversion system present on chromosome I. A previous study has shown that females homokaryotypic for the inversion system produce an excess of heterokaryotypic offspring after mating with a male of each homokaryotype in quick succession. This occurs irrespective of the order of the matings, suggesting that females exhibit cryptic female mate choice for sperm of the opposite karyotype. Here we investigate the mechanism by which females might select sperm by determining if homokaryotypic females have the ability to select sperm on the basis of karyotype after mating with a single heterokaryotypic male. Significantly more heterokaryotypic offspring are produced when homokaryotypic females mate with heterokaryotypic males than in control crosses when heterokaryotypic females mate with homokaryotypic males. Females therefore appear to be capable of selecting sperm from within a single ejaculate to produce fitter heterokaryotypic offspring through cryptic female choice, since intra-ejaculate competition is not predicted to occur according to Hamilton's Rule. In addition, a mass mating experiment reveals that αα homokaryotype females produce significantly more αβ heterokaryotype offspring than αβ or ββ females. These results suggest that αα females can select sperm of the opposite karyotype after mating with only a single heterokaryotypic male and after multiple matings.

20-03 Poster

REPRODUCTIVE SUCCESS OF A POLYMORPHIC INSECT: EFFECTS OF FEMALE GENOTYPE AND RESOURCE AVAILABILITY

Jessica Bots [1], Stefan Van Dongen [1], Luc De Bruyn [2], Hans Van Gossum [1]

[1] *University of Antwerp, Department of Biology, Groenenborgerlaan 171, 2600, Antwerp, Belgium*
[2] *Research Institute for Nature and Forest, Kliniekstraat 25, 1070, Brussels, Belgium*

jessica.bots@ua.ac.be

Sex-limited polymorphism is seen in a variety of species and is usually explained in the context of sexual selection. Particularly when different morphs are only encountered in females, polymorphism is considered to have evolved in response to costly male harassment. Interestingly, in damselflies (Insecta: Odonata) one female morph is very similar in body colouration to the conspecific male while the other (s) is (are) not. These female morphs are expected to receive different amounts of male harassment that may reduce their fitness. Here, we are interested in whether female morphs differ in realised reproductive success measured as fecundity. Usually, fecundity in damselflies is determined by counting the number of eggs in a clutch. Evidently, such a quantitative measure of fecundity may not adequately predict female reproductive success, for example when quality of offspring is variable. We conducted a laboratory rearing experiment with 30 field-caught females (15 of each morph) of a polymorphic damselfly. First, we counted the eggs laid by each female and then we reared offspring to adulthood in one of two food treatments ("abundance" and "stress"). Following, we were able to obtain information on qualitative measures such as hatching success, developmental time and survival of offspring. We will integrate these quantitative and qualitative measures of fecundity to compare the reproductive success of female morphs under different food treatments.

20-04 Poster

EFFECT OF OSR ON MALE COURTSHIP BEHAVIOUR IN THE TWO-SPOTTED GOBY

Karen De Jong [1], Sebastian Wacker [2], Elisabet Forsgren [3], Trond Amundsen [1]

[1] *NTNU, biology, Trondheim, Norway*
[2] *WWU Münster, neuro and behavioural biology, 7491, Münster, Germany*
[3] *NINA, biology, Trondheim, Norway*

karen.de.jong@bio.ntnu.no

Traditionally, animals have been considered to have rather inflexible and "conventional" sex roles: males compete for access to females by courtship and aggression, females are more coy and choosy. However, previous studies have shown that sex roles may vary with mate availability. In the two-spotted goby, a small marine fish, sex roles switch from conventional to reversed during their short breeding season. Males were competitive earlier, females later in the season. This coincided with a dramatic change in sex ratio of ready to mate individuals (OSR). In the present project, we manipulated OSR and density in the lab to assess causal effects on male courtship and aggression. Contrary to prediction, our results suggest that males actually court more when OSR is female-biased, while no effect was found on aggressive behaviour. These results will be discussed along with ongoing fieldwork on the same subject.

20-05 Poster

FEMALE REPRODUCTION COST IN ARRHENOTOKOUS PARTHENOGENESIS SPIDER MITE, TETRANYCHUS URTICAE

Hong T. K. Do [1], Benoît Facon [1], Adrien Frantz [1], Isabelle Oliveri [1]

[1] *Universite Montpellier 2, ISEM, UMR 5554 CNRS, Place Eugène Bataillon, Montpellier, France*

hong.do@univ-montp2.fr

Female reproduction cost of the arrhenotokous parthenogenesis spider mite, ***Tetranychus urticae***, reared on cucumber, was investigated. Fecundity and longevity of unmated, two-mated, and multiple-mated females were measured. Unmated females lived longer than the mated ones, but life time fecundity don't changed significantly. This could be explained by the reproduction cost through mating or/and production of fertilised egg.

Hatchability, larval survival and offspring sex ratio were also recorded. The difference between treatments wasn't significant for hatchability and larval survival. Results suggest the same quality of non-fertilised *vs* fertilised egg. The offspring sex-ratio (proportion of female) was about 0.67 for both two-mated and multiple-mated females.

20-06 Poster

EXPRESSION OF SECONDARY SEXUAL TRAITS IS REDUCED IN THE ABSENCE OF MATE CHOICE IN SALMON

Carlos Garcia de Leaniz [1], Sofia Consuegra [1]

[1] *University of Wales Swansea, Biological Sciences, Singleton Park, SA2 8PP, Swansea, UK*

c.garciadeleaniz@swansea.ac.uk

Artificial propagation in salmonid hatcheries negates the effects of mate choice and sexual selection, but the implications of these for restoration programs are not clear. We examined microsatellite variation, sperm quality and expression of secondary sexual characters in Atlantic salmon spawners of wild and hatchery origin over a 5-year period. We found a positive association between male body size and relative investment in the size of the kype, size of the adipose fin, and breeding colouration suggesting that these are costly, sexually selected traits that may signal male fitness. Hatchery and wild spawners did not differ in heterozygosity, body size, or sperm quality, but males of wild origin invested more on kype size than males derived from hatchery crosses. Thus, if secondary sexual traits are honest indicator of fitness, artificially-bred fish may have inherently lower reproduction success due to lack of mate choice in hatcheries.

20-07 Poster

THE DYNAMICS OF MIXED BREEDING STRATEGY IN A HAPLO- DIPLOID BEETLE

D. Gottlieb [1, 2], Y. Lubin [1], A. Bouskila [2], A. R. Harari [2]

[1] *Ben-Gurion University, Department of Desert Ecology, Blaustein Institute for Desert Research, Israel*
[2] *Ben-Gurion University of the Negev, Department of Life Sciences, Israel*

gdaphna@bgu.ac.il

Theoretical studies focusing on the role of the reproductive assurance strategy in determining the mating system predict that when the probability of finding a mate is low, an inbreeding strategy may be advantageous over the alternative of producing no offspring due to lack of outbreeding possibilities. This should promote a mixed breeding strategy at the individual and population levels. However, the evolutionary significance of the reproductive assurance strategy has been recently questioned, due to the advantage of inbreeding possibly being outweighed by inbreeding depression.

In the date-stone borer beetle, *Coccotrypes dactyliperda* (Fabricus) the haplo-diploid beetles are subject to extreme inbreeding when a virgin female mates with her son and to outbreeding when females disperse and their offspring breed with non-relatives. This system can serve as an exciting model for evaluating the effects of male availability on the mixed breeding system.

Our goals were to examine the effect of male availability on females' decisions, and to compare the results with the predictions of the reproductive assurance strategy. We studied the effect of male availability on C. *dactyliperda* breeding strategy by incorporating mathematical modeling and behavioral experiments. The model investigates the trade-offs between factors affecting decisions of female *C. dactyliperda* regarding optimal waiting time. The model includes a game situation between several females and gives each female the option of inbreeding or waiting for outbreeding opportunities under various male densities.

We found that females sharing a date stone reproduce according to their life history (e.g. age and number of offspring) and male availability. These results support the reproductive assurance hypothesis. We discuss how the model and experiments reinforce each other and emphasize the importance of both male availability and relatedness.

20-08 Poster

LETHAL COMBAT AND SEX RATIO EVOLUTION IN A PARASITOID WASP

Tabitha M. Innocent [1], Joanna Savage [1], Stuart A. West [1], Sarah E. Reece [1]

[1] *University of Edinburgh, Institute of Evolutionary Biology, Ashworth Laboratories, Kings Buildings, West Mains Road, EH9 3JT, Edinburgh, UK*

T.Innocent@sms.ed.ac.uk

Sex allocation theory provides excellent opportunities for testing how behaviour and life histories are adjusted in response to environmental variation. As predicted by Hamilton's local mate competition (LMC) theory, numerous animal species have been shown to adjust offspring sex ratios (proportion male) conditionally, laying less female biased sex ratios as the number of females that lay eggs on a patch increases. Species of the parasitoid genus Melittobia do not respond to LMC and always produce extremely female biased sex ratios. We test whether intense mating competition in the form of fatal fighting between male Melittobia can explain the unusual pattern of sex allocation observed in this genus.

20-09 Poster

LARGE NUMBER OF SPERMATOZOA: AN ADAPTATION TO IMPROVE EFFICIENCY OF SEX IN DIPLOID, BUT NOT HAPLOID ORGANISMS

Jaffe Klays [1]

[1] *Uni Simon Bolivar, Biologia, Caracas, Venezuela*

kjaffe@usb.ve

Explaining the maintenance of sexual reproduction and recombination remains a challenge in biology. The theoretical oddity of sex is based on at least three advantages that asexual organisms have over sexual ones: 1- Asexuals, by not producing males, have a two fold advantage over sexuals, regarding the number of reproductive individuals; 2- Sexuals have an evolutionary disadvantage over asexuals, in that a rare alleles that increases fitness of one parent, for example, is not necessarily transmitted to the offspring, due to segregation. 3- Asexuals do not have to find a mate in order to reproduce. Here I substantiate the proposition that the production of large number of gametes (for example "masting" in massive flowering of trees or spermatozoa of most animals) induces gamete selection which confers very large fitness advantages and thus allows sexual agents using gamete selection to out-breed asexual ones, despite the three disadvantages for sex cited above, if we consider evolution to act on a number of genes simultaneously. Here I show with computer simulations that organisms with haploid males do not profit from an increased number of spermatozoa. The few experimental data on sperm efficiency, i.e. number of sperms produced per new offspring created, seem to support the theoretical results that large number of spermatozoa has an evolutionary advantage for diploid, but not haplodiploid organisms.

20-10 Poster

MECHANISMS PRODUCING SIZE-ASSORTATIVE PAIRING IN THE PEACOCK GUDGEON

Maarit A. Jokinen [1]

[1] *University of Helsinki, Department of Biological and Environmental Sciences, P.O. Box 65, Viikinkaari 1, FI-00014, Helsinki, Finland*

maarit.jokinen@helsinki.fi

Size-assortative pairing is a widely documented phenomenon in animals, but its causes are less clear. The most popular explanation for size-assortative mating is direct male-male competition - large males exclude their smaller rivals from large females. Sometimes competition-hypothesis is just an intuitive assumption and has not been tested against other possible mechanisms: mutual mate choice and physical constraints. I show that size-assortative mating occurs in the peacock gudgeon *Tateurndina ocellicauda* and I test a series of alternative hypotheses to explain how this mating pattern comes about. I find that direct intrasexual competition is not the proximate cause for size-assortativeness in this species. Instead, size-assortative pairing could be a result of mutual mate choice or "prudent choice" (situation where low class individuals choose mates of their own league). Physical constraints might also be involved as this species nests in holes and pairs prefer small nests. This nest preference might explain why small individuals should favor small mates. In addition to that, it can also hinder male-male competition, as large males are not able to use the smallest nest holes.

20-11 Poster

TEMPORAL AVAILABILITY OF FEMALES AND MALE MATING SUCCESS

Maria Järvi-Laturi [1], Kai Lindström [2]

[1] *University of Helsinki, Department of Biological and Environmental Sciences, P.O. Box 65, Helsinki, Finland*
[2] *Åbo Akademi University, Environmental and Marine Biology, 20500, Turku, Finland*

maria.jarvi-laturi@helsinki.fi

Resources and individuals may show spatiotemporal variation. Studies in several taxa suggest that it is difficult for males to monopolize individual females when mating seasons are short and receptive females arrive synchronously. If the asynchrony of other sex increases, the possibility for stolen fertilizations is likely to be higher. Intense competition for mates may then favor the evolution of alternative mating tactics, and not only small sneaker males but also territorial males may try to steal fertilizations. We tested how the genetic mating system differs from the social mating system depending on the female arrival pattern and the OSR. We used the sand goby (*Pomatoschistus minutus*) as a model organism. It has been shown in this species, that the potential for sexual selection can depend on temporal availability of mates and matings are more aggregated to a single male when females arrive asynchronously. When we take a closer look at the mating system, the superiority of the seemingly successful nest-owner male disappears and all male types are players in the mating game. Reproductive success is distributed more evenly among nest-owner males when females arrive in synchrony. Temporal availability of females creates variance in reproductive success among male types in the sand goby.

20-12 Poster

MASSIVE RECRUITMENT EVENT AND EPIFAUNA ATTACKS: DO THEY INFLUENCE SEX CHANGE IN THE PROTANDROUS MOLLUSC, CREPIDULA FORNICATA ?

Sabrina Le Cam [1], Frédérique Viard [1]

[1] *Station Biologique de Roscoff, UMR7144 CNRS UPMC, France*

lecam@sb-roscoff.fr

Theoretical and empirical studies on sequential hermaphrodites showed that size (age) of sex change is influenced by social environment and mating success. We, here, examine sex change dynamics in an invasive protandrous (male then female) mollusc, the slipper limpet *Crepidula fornicata*. Regarding sex change studies, this bentho-pelagic gastropod has an interesting feature: it forms perennial groups of individuals (stacks) in which the timing of sex change depends on the stack sex-ratio. We first investigated the effect of a poorly-studied factor, population dynamics, on the evolution of sexual status through time in one French population. If the recruitment is discrete and strong enough, it should have a shortly delayed effect on the population sex-ratio. Secondly, we studied the prevalence of a boring sponge *Cliona celata*, its effect on reproduction and its temporal evolution according to individual host characteristics in the same population. This endolithic sponge has indeed a detrimental effect on the limpet's shells whose response consists of the production of extra shell material, a costly mechanism. During 32 months, size, sex, female reproductive status and infestation stage by the boring sponge were recorded for 300 individuals sampled monthly in Bay of Morlaix (Brittany). The prevalence of *C.celata* remains stable over time with on average 42.7% of the individuals carrying the sponge. Females were found to be far more infested than males; nevertheless, we did not find any evidence for a cost of producing extra-shells on female fecundity. Consequently, C.celata is unlikely to exert a strong pressure on sex change. At the population level, the sex-ratio– biased towards male as predicted by theory– fluctuated through time with a seasonal variation correlated to the juvenile proportion in the population. Sex change strategies in the slipper limpet thus seem to be influenced not only by local sex-ratio and environmental cues but also by the timing of recruitment and more generally by population dynamics.

20-13 Poster

TRACING SEX-SPECIFIC REPRODUCTIVE CONFLICTS IN BROODING ANTARCTIC ISOPODS USING MICROSATELLITES

Florian Leese [1], Christoph Held [1]

[1] *Alfred Wegener Institute for Polar and Marine Research, Marine Animal Ecology, P.O. Box 12 0161, D-27515, Bremerhaven, Germany*

christoph.held@awi.de

Antarctic marine isopods of the genus *Ceratoserolis* are widespread and significant components of the Antarctic benthic fauna. Members of this genus make large investments into producing their offspring: they grow several years before first reproduction, the eggs hatch and remain inside a brood pouch on the ventral side of the females, after reaching maturity females reproduce at most only every second year, and the fecundity is very low. Under these circumstances, females can be expected to be subject to intense selection to mate with the best males only, whereas males are less restricted and can mate with larger numbers of females. Due to the inaccessibility of the habitat and their extremely long life cycles, there are no direct observations of reproductive behaviour in *Ceratoserolis.*

Using 12 polymorphic microsatellite loci, we have genotyped the offspring inside the brood pouch of 20 ovigerous females and determined whether there is evidence for multiple paternity in a single clutch and whether more than one female in a cohort was fertilized by the same male .

This assignment method has the potential to provide data on reproductive behaviour when no direct observation is possible and has proven useful to infer a potential conflict between the sexes living in an extreme environment.

20-14 Poster

KITTIWAKES CHOOSE MATES THAT ARE GENETICALLY DISSIMILAR

Hervé Mulard [1], Richard H. Wagner [2], Andrew M. Ramey [3], Scott Hatch [3], Etienne Danchin [4]

[1] *Université Pierre et Marie Curie, Laboratoire d'Ecologie, 7 Quai Saint Bernard, 75005, Paris, France*
[2] *Konrad Lorenz Institute for Ethology, Savoyenstrasse 1a, 1160, Vienna, Austria*
[3] *Alaska Science Center, USGS, 1011 East Tudor Road, 99503, Anchorage, U.S.A.*
[4] *Université Paul Sabatier, Laboratoire EDB, 118 Route de Narbonne, 31062, Toulouse, France*

hmulard@snv.jussieu.fr

The genetic bases of mate choice have been the focus of several studies. Females are supposed to choose mates that are genetically dissimilar, or extra-pair partners that are more genetically compatible than their social males. While more and more studies testing this prediction involve genetically polygamous species, few studies concerned genetically monogamous species. In such species, we might expect that mate choice is even more crucial, as there is no opportunities to gain better genes through extra- pair fertilization. However, great frigate birds seem to choose mates that are genetically similar (Cohen & Dearborn 2004), a strange pattern that has not been clearly explained so far. We wanted to know if this was general among monogamous birds. Here we show that Black-legged kittiwakes mate with partners that are genetically dissimilar, apparently to avoid the fitness consequences of inbreeding. Indeed, genetic similarity is negatively correlated to hatching success, and heterozygous chicks have higher survival rates until 25 days old. Thus the genetic bases of mate choice seems to vary among species, and certainly depends on many factors, such as genetic diversity or parental care.

20-15 Poster

COST OF REPRODUCTION IN A SEED BEETLE - A QUANTITATIVE GENETIC PERSPECTIVE

Satu Paukku [1], Janne S. Kotiaho [1], Joseph L. Tomkins [2]

[1] *University of Jyväskylä, Department of Biological and Environmental Science, P.O.Box 35, FI-40014, Jyväskylä, Finland*
[2] *University of Western Australia, School of Animal Biology, WA 6009, Nedlands, Australia*

satupau@bytl.jyu.fi

Life-history theory predicts a trade-off between traits that have an influence on fitness; an example of such trade-off is between reproduction and longevity. In order for the trade-off between reproduction and other life-history traits to evolve, there must be variation in how individuals tolerate the cost of reproduction. We examined the cost of reproduction in male *Callosobruchus maculatus* seed beetles. We found a cost of reproduction that can be seen as reduced longevity. Furthermore, we studied whether the tolerance of cost of reproduction varies between families. We found that there was genetic variation in the tolerance of reproductive costs in *C. maculatus* seed beetle males. A significant interaction between reproductive effort treatment and the genotype on the longevity of males indicated that the variation in tolerating the cost of reproduction has a genetic basis. Moreover, we examined, whether the genetic variation in ejaculate size could be the explaining factor for genetic variation in the cost of reproduction. We show that there is genetic variation in the ejaculate size, and furthermore, covariance between the ejaculate size and longevity. There was also a positive effect of ejaculate size and emergence mass on slope i.e. larger ejaculate indeed can be utilised to prolong life if it is not invested. This means that genotypically differential investment in ejaculates is likely to explain the observation of the genetic variance in tolerating the cost of reproduction in *C. maculatus* males. All these findings suggest that male reproductive effort is far more complex than has traditionally been thought.

20-16 Poster

GENETIC EFFECTS ON MATE CHOICE IN THE SOCIALLY MONOGAMOUS SCARLET ROSEFINCH (CARPODACUS ERYTHRINUS)

Radka Poláková [1, 2], Marta Promerová [2], Michal Vinkler [3], Jan Schnitzer [3], Josef Bryja [2], Tomáš Albrecht [2]

[1] Masaryk University in Brno, Institute of Botany and Zoology, Kotlářská 2, 611 37, Brno, Czech Republic
[2] Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, Studenec 122, 675 02, Studenec, Czech Republic
[3] Charles University in Prague, Viničná 7, 128 44, Praha, Czech Republic

radkpol@centrum.cz

The role of genetic effects in vertebrate mate choice remains a topic of significant interest of evolutionary ecology in general and in sexual selection in particular. There are two main hypothesis of how male selection could operate on the basis of genetic quality: (1) according to the "good genes" hypothesis, all females should prefer the same males bearing the genes increasing fitness, e.g. genes responsible for the resistance against pathogens (MHC genes) whereas (2) "compatibility genes" hypothesis predicts that females should optimize their fitness by choosing the male according to own genotype to avoid inbreeding and increase heterozygosity in offspring. In this study we examine whether allelic variation in MHC class I (exon 3) and genome-wide microsatellite heterozygosity affect social and extrapair mating in the Scarlet rosefinch (*Carpodacus erythrinus*), a socially monogamus songbird with a high percentage (around 30 %) of extra-pair fertilizations (EPFs). We discovered that *Carpodacus* have at least four copies of MHC Class I genes and we also optimized a multiplex set of 20 polymorphic microsatellites for heterozygosity assessment.We compared genetic variation at selectively neutral and MHC loci and compared it between females and their social and extra-pair mates: (1) although it was found that exon 3 of MHC Class I genes is highly polymorphic and variable in *Carpodacus erythrinus,* no evidence was found that this part of MHC affects mate choice and hence reproductive success in this species; (2) analysis of the effect of genome-wide heterozygosity on mating preferences is in progress.

20-17 Poster

GENOMIC CONFLICT OVER SEX ALLOCATION IN THE MEALYBUG PLANOCOCCUS CITRI

Laura Ross [1], David Shuker [2], Ido Pen [1], Franjo Weissing [1], Stuart West [2]

[1] University of Groningen, CEES, Kerklaan 30, 9750 AA, Haren, Netherlands
[2] University of Edinburgh, Institute of Evolutionary Biology, West Mains Road, EH9 3JT, Edinburgh, U.K.

l.ross@rug.nl

Genomic conflict is an important force shaping the evolution of numerous life history traits. Here we consider genomic conflict over sex allocation in the mealybug *Planococcus citri*. Genes expressed in males, females or in their endosymbiotic bacteria all have conflicting interests in the sex ratio of the offspring. Males favour a *female- biased sex ratio*, because due to their genetic system (paternal genome elimination), only their daughters pass on their genes. Females on the other hand may favour a *male-biased sex ratio*. This is because adult females form large immobile colonies, resulting in competition between related females. Mothers should therefore produce more male offspring, reducing competition between their daughters. Lastly, *P. citri* contain symbiotic bacteria. These bacteria are also selected to favour a *female-biased sex ratio*, as they are only transmitted via eggs. Here we test the sex allocation responses of females to different patterns of local resource competition among daughters and consider the role of male and bacterial genomes as a constraint on adaptive sex allocation by female mealybugs.

20-18 Poster

CRYPTIC MALE CHOICE OR EGG COMPETITION?

Gry G. Sagebakken [1], Charlotta Kvarnemo [2], Ingrid Ahnesjö [3], Kenyon Mobley [4], Ines Vilar Gonçalves [2]

[1] Göteborgs University, Department of Zoology, Norbyvägen 18 D, 752 36, Göteborg, Sweden
[2] Göteborgs University, Department of Zoology, Box 463, Göteborg, Sweden
[3] Evolutionary Biology Centre, Dept of Animal Ecology, Box 463, 40530, Uppsala, Sweden
[4] Texas A&M University, Department of Biology, Tamu, USA

gry.sagebakken@zool.gu.se

In fishes with paternal care, filial cannibalism is common. For the behaviour to be adaptive, it is assumed that a cannibalising male increases his lifetime reproductive success by consuming all or parts of the eggs in his care. Filial cannibalism might also be regarded as an expression of male cryptic choice, if the male selectively avoids consuming eggs spawned by preferred females over those spawned by others. Similarly, in the broad-nosed pipefish, *Syngathus typhle*, the male cares for the developing eggs in a brood pouch, and often a subset of the fertilised eggs do not reach parturition. This phenomenon, which is called brood reduction, might be seen as a form of filial cannibalism, at least if the disappeared eggs are absorbed by the male. Another explanation for brood reduction is competition between the eggs of different females: A previous study found that small eggs reared in mixed size broods did significantly poorer than smaller eggs brooded with other small eggs. In the study presented here we tried to determine if there is embryo competition and/or male cryptic choice within the pipefish brood pouch, using eggs labelled with radioactive amino acids. Our results show that amino acids are relocated from the developing embryos, mainly to the father, but to a lesser degree also the other embryos. This means that males of *S. typhle* clearly practice “filial cannibalism”, which might also be cryptic male choice, and that it is possible that embryo competition also takes place.

20-19 Poster

CAN THE LIMITED MARSUPIUM SPACE BE A LIMITING FACTOR FOR FEMALES? INSIGHTS FROM THE INVERTED BROOD POUCH PIPEFISH, SYNGNATHUS ABASTER

Karine Silva [1], Nuno Monteiro [2], Natividade Vieira [1], Vitor Almada [3]

[1] University of Porto, Faculty of Sciences, Praça Gomes Teixeira, 4099-002, Porto, Portugal
[2] University of Fernando Pessoa, Faculty of Sciences, Rua Carlos da Maia 296, 4200-150, Porto, Portugal
[3] ISPA, Rua Jardim do Tabaco 34, 1149-041, Lisboa, Portugal

ksilva@fc.up.pt

Some syngnathids, aside from male pregnancy, show varying degrees of sex-role reversal, with females competing for access to mates and sometimes presenting secondary sexual characters. Energy investment, brooding-space constraints and pregnancy length, operating alone or in combination, may limit female reproductive success, thus allowing for a partial explanation of such sexual differences. Whether these factors can effectively contribute to a sex-role reversal, has not yet been accurately demonstrated, especially in wild populations.

The present work, conducted in a wild population of the sex-role reversed pipefish *Syngnathus abaster*, simultaneously analyzed the space occupied by eggs and the free area in the male’s marsupium. Bimonthly samples were conducted over two consecutive breeding seasons, and the marsupium length as well as the number and average diameter of each male’s eggs were recorded. The number of eggs that would fit in the marsupium unnocupied space was then estimated.

Neither large nor small males presented a fully occupied pouch that would enforce a strong limitation in female reproductive success. Differences in egg number and size between different sized-class males were also observed. Larger individuals received more and larger eggs (which we inferred to be lay by larger females). Interestingly, the largest marsupium unoccupied areas were found in the larger individuals. Altogether these results suggest the existence of assortative mating that may result either from: i) the reluctance of larger males to mate with less quality females, even at the expense of a smaller number of offspring or, ii) female-female competition, that might constraint small females.

20-20 Poster

COMPARATIVE ANALYSIS OF TESTIS PROTEIN EVOLUTION IN RODENTS

Leslie M. Turner [1], Edward B. Chuong [1], Hopi E. Hoekstra [2]

[1] *University of California, San Diego, Biological Sciences, 9500 Gilman Drivc, MC0116, 92093, La Jolla, CA, USA*
[2] *Harvard University, Organismic and Evolutionary Biology, 26 Oxford Street, 02138, Cambridge, MA, USA*

lturner@biomail.ucsd.edu

Reproductive proteins are rapidly evolving in a wide variety of taxa. This pattern applies to proteins that serve diverse functions in both males and females at various stages of the fertilization process. However, many questions remain unanswered, specifically (1) are rates of evolution of reproductive proteins consistently elevated in different taxa? (2) are the same functional classes, genes, and amino acid sites targets of selection in different taxa? (3) are reproductive proteins adaptively diverging in closely related species, at a timescale relevant to reproductive isolation? We address these questions by comparing patterns of evolution of testis-expressed proteins in three lineages of Murid rodents. We compared 2,364 unique expressed sequence tags (ESTs) from testis of the deer mouse (Peromyscus maniculatus) to testis EST sequences from the mouse (Mus musculus) and rat (Rattus norvegicus). Pairwise comparison of homologues allowed us to estimate rates of evolution and identify exceptionally rapidly evolving genes. In all lineages, proteins with testis-specific expression evolve more rapidly than proteins with maximal expression in another tissue. Genes with the highest rates of evolution have a variety of functional roles including sperm motility, DNA binding, and egg-sperm interactions. In some cases, evolutionary rates of genes are consistently elevated in all three lineages, whereas in other cases rapid evolution is lineage-specific. Sequencing of a subset of genes in additional Peromyscus species revealed evidence of positive selection acting on some of these candidates within the genus. Together, these data suggest that adaptive evolution of functionally diverse testis-expressed proteins may contribute to reproductive isolation between closely related species.

20-21 Poster

PARENTAGE AND SIBSHIP INFERENCE FROM GENETIC MARKERS

Jinliang Wang [1]

[1] *Zoological Society of London, Institute of Zoology, Regents Park, NW1 4RY, London, United Kingdom*

jinliang.wang@ioz.ac.uk

Genetic markers have been widely used to infer parentage and thus mating systems, migration and sexual selection in many plant and animal species. Traditional methods infer parentage by calculating the likelihood of a candidate adult (or a pair of candidate adults) being the parent (or parents) of a single child, and ignore any possible relationships (e.g. sibship) among the children. They thus have two major drawbacks. First, the inferred parentage relationships are not necessarily compatible when put together (e.g. a candidate male with genotype AA may be assigned paternity to a child with genotype AB, and a candidate female with genotype AA assigned maternity to the same child. The two pairwise relationships when considered jointly are obviously incompatible with genotype data). Second, the information about parentage extracted from a single child genotype is quite limited. More power could be obtained by using siblings among the children to infer their common parentage. Here I extend my previous likelihood method for sibship reconstruction to allow the joint inference of parentage and sibship in a 2-generation sample of individuals. The power of the method is investigated by simulations. As a demonstration, the method is applied to a cheetah dataset for inferring parentage and mating systems.

20-22 Poster

CONDITION-DEPENDENT GENE EXPRESSION BETWEEN THE SEXES

Minyoung Wyman [1], Locke Rowe [1], Aneil Agrawal [1]

[1] *University of Toronto, Ecology & Evolutionary Biology, 25 Harbord Street, Toronto, Canada M5S 3G5*

minyoung.yi@utoronto.ca

The degree of trait expression relies upon an individual's quality; this is known as condition dependence. While most traits demonstrate condition dependence, sexually selected traits are especially sensitive to condition. High condition males will allocate more to sexually selected traits when compared to low condition males. This expectation has been observed for morphological traits. We examined the effect of condition on the expression of genes related to mating and courtship in Drosophila melanogaster. We reared flies on low and high nutrition food. We used microarrays to analyze differences in expression patterns between low and high food reared individuals. We tested the hypothesis that genes related to mating success have greater condition dependent expression when compared to genes not related to mating success. We also used microarrays to identify genes that have greater condition dependent expression in males relative to females and the converse. These genes may be important in elucidating the potential link between condition dependence and sexual dimorphism.

Floral evolution: mechanisms behind shifts in pollination strategies

21

Saturday August 25 *Location*: Ekonomikum 4

Symposium 21: Floral Evolution: mechanisms behind shifts in pollination strategies

ORGANIZERS: Johanne Maad, Uppsala University, Sweden
Miguel Rodriguez-Girones, CSIC, Almeria, Spain

14.00-14.30	**Steven Johnson** (invited) Patterns and processes of pollinator-driven plant diversification
14.30-15.00	**Elizabeth Elle** (invited) Floral evolution and mating system shifts: selection by pollinators and climate
15.00-15.20	**Rodrigo Medel** Disentangling the complexity of pollinator-mediated selection
15.20-15.50	*Coffee*
15.50-16.10	**Eric Imbert** Flower colour polymorphism in Iris lutescens : does the colour matter?
16.10-16.30	**Per Toräng** Mutualists and antagonists mediate frequency dependent reproductive success in a diamorphic herb
16.30-16.50	**Luc Gigord** Can rewardlessness be an ESS...? An in situ experimental test using the food-deceptive European orchid Himantoglossum robertianum
16.50-17.10	**Katja Hogendoorn** Biogeography of Australian bees and evolution of flower morphology

21-01 Talk

PATTERNS AND PROCESSES OF POLLINATOR-DRIVEN PLANT DIVERSIFICATION

Steven D. Johnson [1]

[1] *University of KwaZulu-Natal, School of Biological and Conservation Sciences, P Bag X01, Scottsville, Pietermaritzburg 3209, South Africa*

JohnsonSD@ukzn.ac.za

Adaptations to animal pollinators have resulted in striking patterns of floral diversification within, and convergence between, angiosperm lineages. Pollinator-related floral syndromes, once associated with an arcane typological approach, are being studied afresh using a combination of multivariate and phylogenetic methods. However, the causal links, if any, between these floral adaptations and plant speciation remain contentious. In the Grant-Stebbins model, local adaptation to a geographical mosaic of pollinators drives floral diversification, and this results, ultimately, in reproductive isolation. Although some have suggested a role for reinforcement in this process, this is considered unlikely on theoretical grounds. Available evidence suggests that flowers evolve mainly through selection for traits that alleviate pollen limitation or enhance pollen dispersal, and only very rarely through selection for traits that reduce hybridization.

21-02 Talk

FLORAL EVOLUTION AND MATING SYSTEM SHIFTS: SELECTION BY POLLINATORS AND CLIMATE

Elizabeth Elle [1]

[1] *Simon Fraser University, Dept. of Biological Sciences, 8888 University Drive, V5A 1S6, Burnaby, BC, Canada*

eelle@sfu.ca

Floral traits can predict the mating system, with small-flowered forms normally having higher selfing rates than large-flowered forms. Higher selfing rates may result from reduced attractiveness to pollinators coupled with passive autogamy due to the close proximity of sexual parts in small flowers. Small flowers may evolve as a resource savings in environments where pollinators are rare, if autonomous selfing is favored because it provides reproductive assurance. Though considered less often, small flowers may also evolve due to selection pressures independent of the pollination environment. Here, I present data on how the pollination environment and the abiotic environment affect the combination of flower size and autonomous selfing ability in *Collinsia parviflora*. Pollinator visitation to small-flowered populations is low, and these populations derive a greater reproductive assurance benefit from selfing than large-flowered populations with high visitation. Relatively smaller populations (within flower size) also have lower visitation and greater benefit of selfing. Small-flowered populations, however, are found in drier, ephemeral habitats that cease to support plant growth earlier than the wetter habitats where large-flowered populations are found, suggesting they may be under strong selection for early reproduction. In a selection experiment, I demonstrate that selection for earlier flowering results in plants with smaller flower sizes and higher autonomous selfing rates. Thus, the long-standing observation that selfing forms are often found in marginal habitats may be due not only to the unpredictable pollination environment in these marginal areas, but also to the sub-optimal abiotic environment. Considering a greater variety of the ecological selection pressures experienced by plant populations would greatly improve our understanding of the mechanisms of floral differentiation and their importance for both mating system shifts and speciation.

21-03 Talk

DISENTANGLING THE COMPLEXITY OF POLLINATOR-MEDIATED SELECTION

Rodrigo Medel [1], Carezza Botto-Mahan [1]

[1] *University of Chile, Department of Ecology, Las Palmeras 3425, Santiago, Chile*

rmedel@uchile.cl

Studies of pollinator-mediated selection performed during the last 20 years have provided strong evidence that pollination is the main ecological force underlying the evolution of the flower phenotype. Flower change, however, is the macroscopic net result of an essentially complex phenomenon that includes, among other factors, the nonadditive impact of pollinators on plant fitness. As a consequence, the expected flower change is difficult to predict from the simple presence or absence of specific pollinator taxa. In this study, we examine the relative contribution of bees and hummingbirds to the net pollinator-mediated selection acting upon the Andean monkeyflower Mimulus luteus. Our results revealed significant nonadditive selective effects of bees and hummingbirds on some components of the flower phenotype, indicating that the selective impact of one taxa is contingent on the presence or absence of the other. Because bees and hummingbirds have divergent effects on the flower phenotype, contingent rather than consistent selection seem to underly flower divergence in the Mimulus complex in southern South America.

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21-04 Talk

FLOWER COLOR POLYMORPHISM IN IRIS LUTESCENS : DOES THE COLOR MATTER ?

Eric Imbert [1]

[1] *Université Montpellier II, 34095, Montpellier, France*

eric.imbert@univ-montp2.fr

Flower color is a key feature in the plant/insects relationships, in particular for the attractivity of pollinators. As a consequence, this character is submitted to stabilizing selection, and most species show a narrow intraspecific variability. However, some species such as *Viola lutea*, *Dactylorhiza sambucina* or *Iris lutescens* are polymorphic. The maintenance of polymorphism for traits under a high selective pressure is a recurrent question in evolutionary biology. Negative frequency-dependent selection is one mecanism explaining this polymorphism.

Iris lutescens (Iridaceae) is a common species in Mediterranean communities that has a striking purple-yellow flower color polymorphism. It can also be found some intermediate phenotypes. To test the negative frequency-dependent selection hypothesis, I conducted in 2006 and 2007 a set of observations about pollinator attractivity and fruit set in naturel populations. In this talk, I will present the results of these observations, and discuss about flower color in this species.

21-05 Talk

MUTUALISTS AND ANTAGONISTS MEDIATE FREQUENCY DEPENDENT REPRODUCTIVE SUCCESS IN A DIMORPHIC HERB

Per Toräng [1], Johan Ehrlén [2], Jon Ågren [1]

[1] *Uppsala University, Ecology and Evolution, Villavägen 14, 752 36, Uppsala, Sweden*
[2] *Stockholm University, Botany, 106 91, Stockholm, Sweden*

per.torang@ebc.uu.se

Conspicuous traits that increase attractiveness to mutualists and mates may negatively affect reproductive success in the presence of antagonists. In plants, stature, the number, size and arrangements of flowers, and nectar production can influence reproductive success through effects mediated by both pollinators and predators. With conflicting selection pressures, the maintenance of alternative reproductive strategies can be explained by either frequency-dependent selection or environment-dependent selection. We combined field experiments and surveys of natural populations to determine whether selection on floral display is frequency-dependent in the self-incompatible perennial herb *Primula farinosa* L. (Primulaceae), which is polymorphic for inflorescence height and occurs in a short-scaped and a long-scaped morph. Among short-scaped, but not among long-scaped plants, both the initiation of fruits and seeds and seed predation were positively correlated with the frequency of the long-scaped morph. The relative strength of these effects and therefore their net outcome varied among years and populations. Our results suggest that both mutualists and antagonists may mediate frequency-dependent selection, and that the range of characters subject to frequency-dependent selection may be wider than previously appreciated.

21-06 Talk

CAN REWARDLESSNESS BE AN ESS...? AN IN SITU EXPERIMENTAL TEST USING THE FOOD-DECEPTIVE EUROPEAN ORCHID HIMANTOGLOSSUM ROBERTIANUM

Luc D. B. Gigord [1], Ann Smithson [2]

[1] *University of Lausanne, Ecology and Evolution, DEE, Biophore, 1015, Dorigny, Suisse*
[2] *York, UK*

Luc.Gigord@unil.ch

Many species of orchids are entirely rewardless, offering their pollinators neither nectar nor pollen reward in return for visitation. Since plant-pollinator interactions are usually perceived as mutualistic, the existence and persistence of such a deceptive pollination strategy in so many species has long puzzled evolutionary biologists. Indeed Darwin argued that it was evolutionarily impossible. Here we show experimentally that rewardlessness is an evolutionarily stable strategy in the rewardless Mediterranean orchid Barlia robertiana through an advantage via outcross male reproductive success, and we predict that the rewardless strategy would spread to fixation in this species from a hypothetical population of nectar reward producers.

21-07 Talk

BIOGEOGRAPHY OF AUSTRALIAN BEES AND EVOLUTION OF FLOWER MORPHOLOGY

Remko Leijs [1], Katja Hogendoorn [2]

[1] *South Australian Museum, Evolutionary Biology Unit, North Terrace, SA 5000, Adelaide, Australia*
[2] *University of Adelaide, School of Agriculture, Food and Wine, SA 5005, Adelaide, Australia*

katja.hogendoorn@adelaide.edu.au

The Australian flora differs from that of other continents in its abundance of flowering plants that are pollinated by birds and mammals.

To analyse the possible evolutionary causes behind this phenomenon, we investigate the biogeography of Australian bees, the major group of pollinators, that is thought to drive speciation and the evolution of flower morphology. We use recently published molecular phylogenies and molecular clock dating to address timing of arrival and biogeographical patterns of dispersal of the major Australian bee groups. The two possibilities specifically addressed are vicariance since the break-up of Gondwanaland 80 Mya, after which the continent started to move northwards, and arrival through dispersal from other continents.

We show that the representatives of 4 out of 5 bee tribes arrived independently into Australia through dispersal shorter than 20 MYA. This recent influx of bee groups coincides with Australia's vicinity to SE Asia. The short-tongued colletid bees, comprising 50% of the Australian native bee species, are the only group whose presence is better explained by vicariance. It is therefore likely that the flower morphology of major Australian plant groups evolved during an extended period of absence of long-tongued bees. This hypothesis is supported by the correlation between the timing of the radiations in the peas, a group that depend on long-tongued insects for pollination, and the influx of long-tongued bees.

21-01 Poster

COMPARISON WITH ORIGINAL NATIVE SENECIO TAXA REVEALS CRYPTIC MATING SYSTEM CHANGES IN THE SELF-INCOMPATIBLE INVASIVE PLANT, SENECIO SQUALIDUS L. (ASTERACEAE)

Adrian C. Brennan [1], Stephen A. Harris [2], Simon J. Hiscock [3]

[1] *University of St Andrews, School of Biology, Mitchell Building, KY16 9TH, St Andrews, Fife, UK*
[2] *University of Oxford, Department of Plant Sciences, South Parks Road, OX1 3RB, Oxford, UK*
[3] *University of Bristol, School of Biological Sciences, Woodland Road, BS8 1UG, Bristol, UK*

adrian.brennan@bristol.ac.uk

In the 300 years since Senecio squalidus was introduced from Mt. Etna, Sicily, it has rapidly spread to colonise most urban areas in Britain. Spatial isolation in the new invasive range has led to adaptive divergence in British S. squalidus to the extent that it is recognised as a new diploid species distinct from original Mt. Etna hybrid zone Senecio taxa. Throughout this rapid colonisation, S. squalidus has retained an outcrossing mating system based upon sporophytic self-incompatibility (SSI), contrary to observations that colonists are often selfing (Baker's Rule). Self-incompatibility in Asteraceae is controlled by a single S locus expressing pollen and pistil allele-specific recognition factors and negative-frequency-dependent selection results in high S allele polymorphism over evolutionary time. Mating system studies of British S. squalidus populations have confirmed that SSI is typically strongly expressed but that it is made up of relatively few, dominantly interacting S alleles reflecting the population bottleneck associated with introduction and subsequent mating system changes to improve mate availability. Here we present the results of additional mating system studies of closely related Senecio taxa from Mt. Etna, Sicily. Comparisons with related Sicilian Senecio taxa permit direct tests of hypotheses about mating system changes associated with invasiveness in British S. squalidus including: 1) No loss in strength of expression of SSI has been necessary to promote invasive success; 2) S allele polymorphism (and consequently, mate availability) has been reduced; 3) Increased S allele dominance interactions that improve mate availability have been favoured.

21-02 Poster

A GEOGRAPHIC MOSAIC OF COEVOLUTION IN A GENERALIZED PLANT-POLLINATOR SYSTEM

José María Gómez [1], Francisco Perfectti [2], Jordi Bosch [3], Juan Pedro M. Camacho [2]

[1] *Universidad de Granada, Departamento de Ecología, Avda. Fuentenueva s/n, 18071, Granada, Spain*
[2] *Universidad de Granada, Departamento de Genética, Avda. Fuentenueva s/n, 18071, Granada, Spain*
[3] *Universitat Autònoma de Barcelona-CREAF, Departament de Biologia Animal, Biologia Vegetal y Ecologia, Bellaterra, 08193, Barcelona, Spain*

jpmcamac@ugr.es

Geographical mosaic of coevolution is manifested by significant variation among populations in the ecological and evolutionary outcomes of the interactions. In order to study coevolutionary interactions at a local level, we analyse here a number of morphological traits (including flower shape and several measures of flower and plant size), herbivory rate and pollinator visitation rate in eight natural populations of the plant *Erysimum mediohispanicum* (Brassicaceae), to explore their association with female fitness (measured as total number of seeds). Selection was estimated by using two standard methodologies: selection gradients and structural equation modelling. We found that different populations were under different selective regimes. The traits affected by selection varied depending on the predominant local pollinators. We also found that the potential for pollinator-mediated selection was strongly affected by the intensity of mammal herbivory, resulting in populations with strong selective regime (hot spots) intermingled with populations with weak selective regimes (cold spots). This outcome suggests the occurrence of a mosaic of selection for *E. mediohispanicum* in the Spanish Sierra Nevada shaped by the interactions maintained with both mutualists and antagonist organisms.

21-03 Poster

GEOGRAPHICALLY VARIABLE COEVOLUTION IN A WIDESPREAD PLANT-POLLINATOR INTERACTION

Anna-Liisa Laine [1], John N. Thompson [2], Catherine C. Fernandez [2]

[1] *University of Helsinki, Department of Biological and Environmental Sciences, Finland, University of Helsinki, PO Box 65 (Viikinkaari 1), 00014*
[2] *University of California, Department of Ecology and Evolutionary Biology, 95064, Santa Cruz, California, USA*

anna-liisa.laine@helsinki.fi

Recent coevolutionary theory has indicated that the geographic structure of species has the potential to impose powerful but geographically variable effects on coevolving species. The interaction between the pollinating floral-parasitic moth *Greya politella* (Prodoxidae) and its *Lithophragma* (Saxifragaceae) host plants is widespread in western North America. Ongoing studies have documented striking geographical variation in the strength and direction of coevolution between the moth and its host plants as the ecological outcomes range among habitats from mutualism to antagonism. This variation is driven by differences in the composition and abundance of co-pollinators. At the southern edge of the range some moth populations have acquired a novel endemic host species, *Lithophragma cymbalaria*. At these sites *G. politella* co-occurs with a closely related species, *Greya obscura*, a potential cheater in the interaction. In a situation where co-pollinators are rare, together the two moth species have a synergistic effect on their host plant. Hence, the evolution of *Lithopragma* host plants can only be understood in a geographic context of spatially variable selection imposed by its pollinators.

21-04 Poster

POLLINATOR SHIFTS AND EVOLUTION OF SPUR LENGTH IN THE MOTH-POLLINATED ORCHID PLATANTHERA BIFOLIA

Elin Boberg [1], Ronny Alexandersson [2], Johanne Maad [1], Jon Ågren [1], L Anders Nilsson [1]

[1] *Uppsala University, Ecology and Evolution, Uppsala, Sweden*
[2] *Uppsala University, Uppsala, Sweden*

johanne.maad@ebc.uu.se

Geographic variation in the composition of the pollinator fauna may give rise to differences in pollinator-mediated selection on floral traits and the evolution of intraspecific variation in flower morphology. If a close morphological fit between flower and pollinator is crucial for effective pollination, a correlation between the morphology of the flower and of the dominating pollinator is expected. We investigated geographical variation in the length of the floral spur in the moth-pollinated orchid *Platanthera bifolia* in relation to variation in the pollinator fauna across Sweden and Norway. The length of the spur varied among regions and also among habitats within one of the regions studied. Spur length was positively correlated with the length of the proboscis of local pollinators. The results are consistent with the hypothesis that intraspecific variation in spur length reflects adaptive evolution in response to selection exerted by the locally most important pollinator.

21-05 Poster

MOLECULAR MECHANISM(S) UNDERLYING THE POLYPHYLETIC ORIGIN OF THE INFLATED-CALYX-SYNDROME (ICS) IN SOLANACEAE

Simone Riss [1], Chaoying Y. He [1], Britta Grosardt [1], Jinyong Y. Hu [1], Muhammad R. Khan [1], Heinz Saedler [1]

[1] *Max Planck Institute for Plant Breeding Research, Molecular Plant Genetics, Carl-von-Linné-Weg 10, 50829 Cologne, Germany*

riss@mpiz-koeln.mpg.de

The origin of morphological novelties is a long-standing problem in evolutionary biology. In Physalis the sepals resume growth after pollination and form a lantern-like structure, which encapsulates the mature fruit. This morphological novelty is termed “Inflated-Calyx-Syndrome” (ICS) or “Chinese lantern”. ICS formation in Physalis floridana is conditioned by heterotopic expression of the MADS-box transcription factor MPF2 in floral organs, where it promotes calyx cell division. In contrast, its ortholog STMADS16 in the non-ICS plant Solanum tuberosum (potato) is only expressed in vegetative tissues. The recruitment of MPF2 into a floral program during the evolution of the “Chinese lantern” in Physalis was probably mediated by promoter changes. However, signals, such as hormones produced during or after fertilization, are also essential for the ICS; gibberellin is needed for cell elongation and cytokinin for the nuclear transport of the MPF2 protein and thus promoting calyx cell division.

Surprisingly, at least five genera have evolved ICS or ICS-like calyces within the family of Solanaceae. Thus, in spite of the complexity of the mechanism resulting in ICS, ICS formation seems to be a polyphyletic trait. In this project the molecular mechanism(s) of the polyphyletic origin of the ICS in Solanaceae, especially cis-regulatory elements (and trans-acting factors) controlling heterotopic expression of MPF2-like genes in Solanaceae, are studied.

21-06 Poster

FORBIDDEN LINKS OR NEUTRAL EFFECT? ON THE RELATIVE IMPORTANCE OF PHENOTYPIC TRAITS AND LOCAL SPECIES ABUNDANCE FOR THE ECOLOGY AND EVOLUTION OF PLANT-POLLINATOR INTERACTIONS

Luis Santamaria [1], Miguel A. Rodriguez-Girones [2]

[1] *Mediterranean Insitute for Advanced Studies (IMEDEA), Natural Resources, Miquel Marques 21, 07190, Esporles, Spain*
[2] *Estacion Experimental de Zonas Aridas, General Segura, 1, 04001, Almeria, Spain*

luisesant@yahoo.com

Recent attempts to examine the biological processes responsible for the general characteristics of mutualistic networks focus on two types of explanations: non-matching biological attributes of species that prevent the occurrence of certain interactions (“forbidden links”), generated by coevolutionary processes, and random interactions among individuals that are proportional to their abundances in the observed community (“neutrality hypothesis”). Because these hypothesis differ in their mechanistic explanation of network assemblage, they have fundamentally different implications for the evolution of plant and pollinator traits. However, recent evidence suggest that both process may modulate each other in a more fundamental way than previously recognized. On the one hand, the generation of right-skewed distributions of species´ degree of specialization (number of interspecific interactions, *s*) using forbidden-links models suggest that such distribution may arise from the network pattern of species interactions (i.e. generalist species may be locally abundant because they are able to exploit more floral resources). On the other hand, recent models addressing the effect of floral traits on flower exploitation by pollinators indicate that the relative abundances of floral morphs and pollinator types have important consequences for the degree of generalism shown by each plants and pollinator type (i.e. locally abundant species tend to behave as generalists). The interplay between these two processes will chiefly depend on the spatial and temporal scales at which plant and pollinator abundances vary, and the spatial scale at which pollinators perceive and exploit floral resources.

21-07 Poster

THE NEGATIVE INFLUENCE OF POLLINATOR LIMITATION AND FLORAL HERBIVORY ON THE SEED SET OF A BIENNIAL PLANT INCREASES WITH POPULATION SIZE

Virve Sõber [1], Tiit Teder [1], Mari Moora [1]

[1] *University of Tartu, Institute of Botany and Ecology, Lai 40, 51005, Tartu, ESTONIA*

virve.sober@ut.ee

Plants can experience the effect of habitat fragmentation directly as well as indirectly, through its effects on the species with which they interact. Studies on plant reproductive response to fragmentation that include different interactions are rare.

We examined (1) how the levels of pollinator visitation and floral herbivory vary with the population size, and (2) how these factors affect the seed set of *Verbascum nigrum* (Scrophulariaceae). The latter is a self-incompatible biennial herb that prefers disturbed habitats and grows in relatively discrete populations that vary in size.

Higher levels of floral herbivory reduced seed set remarkably, whereas higher levels of pollinator visitation increased it. There were more plants with floral herbivores but less pollinator visits per plant in larger *V. nigrum* populations. Our results imply that the net effect of these two interactions might lead to lower seed set in larger *V. nigrum* populations.

21-08 Poster

THE RELATIONSHIP BETWEEN BREEDING SYSTEM AND SEED SIZE IN A NEOTROPICAL FLORA: TESTING EVOLUTIONARY HYPOTHESES

Steven M. Vamosi [1], Susan J. Mazer [2], Fernando Cornejo [3]

[1] *University of Calgary, Biological Sciences, 2500 University Drive NW, T2N1N4, Calgary, Canada*
[2] *University of California Santa Barbara, Department of Ecology, Evolution and Marine Biology, 93106, Santa Barbara, USA*
[3] *Amazon Conservation Association, Jiron Cusco 499, Madre de Dios, Peru*

smvamosi@ucalgary.ca

A well-known, but largely untested, prediction in plant reproductive ecology is that dioecious taxa produce larger seeds than their cosexual counterparts. Using a data set comprised of 964 species representing the flora of the Tambopata Wildlife Reserve (Madre de Dios, Peru), we evaluated the ecological and evolutionary relationships between breeding system and mean seed size. We conducted cross-species and evolutionary analyses. In both analyses, we controlled for potentially confounding effects of life form by examining these relationships within woody taxa, trees alone, and non-woody taxa. To our knowledge, this is the first study to account for evolutionary relationships and life form in an analysis of associations between breeding systems and seed size. Cross-species analyses detected that (1) among woody species, among lianas, among shrubs, and among all species pooled, dioecious species produced larger seeds than cosexual taxa. Phylogenetically independent contrasts (PICS) between sister taxa detected: (2) that dioecious clades tended to have larger seeds than their nondioecious counterparts, but (3) no consistent difference in seed size between hermaphroditic and monoecious sister taxa, when all life forms were pooled; (4) no highly significant association between breeding system and seed mass among woody taxa (based on sign tests), although contrasts supported the prediction that dioecious taxa have larger seeds than nondioecious taxa; and (5) no relationship between breeding system and seed mass within trees and shrubs.

21-09 Poster

POLYPLOIDY AND THE TRANSITION BETWEEN SELF-INCOMPATIBILITY AND SELFING: THEORETICAL EXPECTATIONS, EVOLUTIONARY PATTERNS AND GENETIC VARIATION AT THE S-LOCUS IN RORIPPA (YELLOWCRESS).

Peter Van Tienderen [1], Marc Stift [1], Walter Bleeker [2], Pieternella Luttikhuizen [1]

[1] *University of Amsterdam, Institute for Biodiversity and Ecosystem Dynamics, Kruislaan 318, 1098 SM, Amsterdam, Netherlands*
[2] *University of Osnabrueck, Osnabrueck, Germany*

tienderen@science.uva.nl

The combination of a doubled genome and self-incompatibility appears to be a very bad one: on the one hand the number of potential partners of tetraploid outcrossers is severely reduced, and on the other hand the need to remain incompatible is limited, as inbreeding depression is less important in tetraploids due to the masking of deleterious genes. This leads to the expectation that the evolution of polyploidy is often coupled to a change in mating system toward selfing, and thus that polyploids have a different pollination strategy than diploids. We address this issue by three approaches. First we test whether there is any evidence of concerted evolution of polyploidy and selfing, using a phylogenetic approach. Using Pagel's DISCRETE program we find that there is indeed a strong evolutionary signal in the Rosaceae, but no trend in the Brassicaceae. However, this pattern can be explained by the different mechanisms of the SI system (gametophytic and sporophytic, respectively), rather than by a difference in pollen limitation or any effects of inbreeding depression. We then model the variability at the S-locus to see how much variation is required and maintained to circumvent pollen limitation in self-incompatible tetraploids. It appears that dominance relations among S-alleles play a crucial role in increasing the fraction of compatible pollen for tetraploids. Finally we look at the actual amount of variation at the S-locus in diploid and tetraploid Rorippa amphibia (Brassicaceae). We find that the variation is comparable, suggesting that the tetraploids have picked up most of the variation from diploid R. amphibia or perhaps by hybridisation with related tetraploid species such as R. sylvestris. At least for R. amphibia the transition to polyploidy appears not to incur a change in flower morphology or pollination strategy; the generality of this result is discussed.

21-10 Poster

POWER IN EXPERIMENTAL SELECTION STUDIES

Didrik Vanhoenacker [1]

[1] *Stockholm Univeristy and Södertörn University College, Dept. of Botany, Stockholm, SE-106 91, Sweden*

didrik@botan.su.se

Power in studies of natural selection is often problematic. Selection can be very weak and is usually obscured by environmental effects. Still, it can be biologically important over evolutionary times. Therefore, to detect natural selection often requires large sample sizes. As a consequence many selection studies have been criticized for low power. Selection by some agents, e.g., grazers, are sometimes relatively straight-forward to quantify in descriptive studies. However, in many cases an experimental approach is needed with exclusion of the selective agent (e.g., herbivores or parasites) or manipulation, such as hand-pollination or cutting of plants. This creates experimental setups with an ancova or a two-way anova design, with trait and treatment as explanatory variables. The idea is of course that the treatment will remove selection, resulting in a trait × treatment interaction effect. Despite the lack of power tests for more complicated (or even simple!) designs in most statistical packages, computational power today makes it easy to simulate power also for higher-order interactions. I have studied how the required sample size changes as one moves to more complicated designs. Let's consider a fictive plant species with either blue or white flowers, where the blue-flowered plants seem to be better pollinated. A pilot study showed that a descriptive study with 40 blue-flowered and 40 white-flowered plants would have a power of 80% to detect a 5% difference in seed set. But, to rule out resource limited abortion one would like to conduct a hand-pollination experiment and aim for the interaction colour × pollination treatment. How many plants would be required to maintain the power of 80%? 40 blue-flowered and 40 white-flowered? 80 blue-flowered and 80 white-flowered? Or even more plants?

Process and implications of phenotype-dependent dispersal and settlement

22

Saturday August 25 *Location*: University building X

Symposium 22: Process and implications of phenotype-dependent dispersal and settlement

ORGANIZERS: Pim Edelaar, Texas A&M University, USA
Jean Clobert, Université Pierre et Marie Curie, France

14.00-14.30 **Dan Bolnick** (invited)
Examining adaptive variation at multiple spatial scales in threespine stickleback

14.30-15.00 **Ben Sheldon** (invited)
Natal environment, dispersal, and the impermanence of
environmental effects in the great tit

15.00-15.20 **Audrey Chaput-Bardy**
Morphological clines and consequences on dispersal in dendritic landscapes

15.20-15.50 *Coffee*

15.50-16.10 **Marjo Saastamoinen**
Spatial variation in dispersal rate and related life history
traits in a butterfly metapopulation

16.10-16.30 **Fabrice Eroukhmanoff**
Habitat choice, phenotype–dependent dispersal and parallel
evolution in a freshwater isopod

16.30-16.50 **Jean-François Le Galliard**
Influence of past and present environments on natal dispersal
behaviour in small mammals

16.50-17.10 **Julien Cote**
Social personalities influence natal dispersal and fitness outcomes in
common lizard (Lacerta vivipara)

22-01 Talk

EXAMINING ADAPTIVE VARIATION AT MULTIPLE SPATIAL SCALES IN THREESPINE STICKLEBACK

Daniel I. Bolnick [1]

[1] *University of Texas at Austin, Section of Integrative Biology, One University Station C0930, 78712, Austin, TX, USA*

danbolnick@mail.utexas.edu

Recently, there has been renewed appreciation for the role of adaptive habitat choice in facilitating population divergence among different habitats. Such phenotype-dependent dispersal may counteract the traditional view that dispersal increases similarity among populations. The effects of adaptive habitat choice will presumably be highly dependent on spatial scale, in particular how fine-grained the habitat variation is relative to movement rates of the focal organism. Here, I illustrate the role of spatial scale with an analysis of phenotypic and ecological divergence in a population of threespine stickleback in British Columbia. The stickleback inhabit a lake that is subdivided into two basins (one very shallow, the other quite deep), connected by a narrow channel (1 m wide) that permits extensive movement. I show that fish in the two basins use different prey, and are isotopically as different as the well-known benthic/limnetic species pairs found in some other lakes. Despite this ecological divergence, there is negligable phenotypic divergence despite ongoing divergent selection. Tese results suggest that phenotype-dependent habitat choice has little effect, and classic migration-selection balance is operating. Similarly, there is no evidence for morphological differentiation between deep and shallow habitats within the larger basin, though there is evidence for habitat preferences. Finally, at the smallest spatial scale (of individual fish), there is substantial evidence for phenotype-dependent niche partitioning within the population. This fine-scale variation arises not from spatial structure of the population, but from individual-level variation in resource use (‘individual specialization’). Hence, in stickleback it appears that adaptive habitat choice does not drive between-site or between-habitat divergence. Rather, it leads to individual level variation that has no detectable effect on geographic variation.

22-02 Talk

NATAL ENVIRONMENT, DISPERSAL, AND THE IMPERMANENCE OF ENVIRONMENTAL EFFECTS IN THE GREAT TIT

Ben C. Sheldon [1]

[1] *University of Oxford, EGI, Department of Zoology, UK*

ben.sheldon@zoo.ox.ac.uk

The interaction between environmental variation, individual phenotypic differences, and dispersal behaviour provides many potential insights into the causes and consequences of individual variation. Non-random dispersal has the potential to both increase and reduce spatial differences among individuals: the extent to which individuals carry ‘phenotypic imprints’ of their natal environment is an important determinant of the long-term consequences of non-random dispersal. I will describe analyses of the influence of natal environment on dispersal, survival and subsequent life history variation from a sample of >5000 individual great tits studied over 40 years in a heterogeneous environment. Strong environmental effects were readily detected, but in contrast to many other recent studies of wild populations, these effects were not readily transmitted across generations for short-distance dispersers. In contrast, long-distance dispersers apparently possessed permanent environmental imprints. I will discuss the implications of these two findings for our understanding of local adaptation and population structuring in heterogeneous environments.

22-03 Talk

MORPHOLOGICAL CLINES AND CONSEQUENCES ON DISPERSAL IN DENDRITIC LANDSCAPES

Audrey Chaput-Bardy [1], Christophe Lemaire [1], Arnaud Grégoire [2], Jean Secondi [1]

[1] *Angers Unviversity, Laboratoire Paysages et Biodiversité, UFR Sciences, 2 bd Lavoisier, 49045, Angers cedex 01, France*
[2] *Montpellier II University, UMR 5175 Centre d'Ecologie Fonctionnelle et Evolutive, 1919 route de Mende, F34293, Montpellier cedex 5, France*

audrey.chaput-bardy@univ-angers.fr

In complex landscapes such as river networks, organisms face gradients in geomorphological, water, ecological or landscape characteristics at the catchment scale. These environmental variables often determine developmental conditions for larval stages and influence adult phenotypic characteristics of freshwater insects. Hence, ecological clines are expected to generate gradual geographical changes in morphology-dependent life history traits, particularly those associated to dispersal. We analysed morphological variations in the banded damselfly, *Calopteryx splendens* (Odonata-Zygoptera) in the middle Loire drainage in France. We observed a body size gradient, individuals being larger in the lower and warmer reaches of the river network. Such a morphological cline is expected to generate an asymmetric downstream-upstream flow of individuals as larger individuals, in insects, often disperse farther and ultimately to influence the overall population genetic structure at the catchment scale. We addressed this issue using two complementary approaches. We first carried out a dispersal study using capture-recapture method in downstream individuals with large body size and in upstream individuals with small body size from the same tributary. Second, we carried out genetic analyses to estimate gene flow within and among watercourses of the catchment.

22-04 Talk

SPATIAL VARIATION IN DISPERSAL RATE AND RELATED LIFE HISTORY TRAITS IN A BUTTERFLY METAPOPULATION

Marjo Saastamoinen [1], Ilkka Hanski [1]

[1] *University of Helsinki, Department of Biological and Environmental Sciences, PO Box 65, 00014, Helsinki, Finland*

marjo.saastamoinen@helsinki.fi

Long-term persistence of classic metapopulations requires sufficient dispersal to establish new local populations to compensate for local extinctions. In the Glanville fritillary butterfly (*Melitaea cinxia*), females establishing new populations especially at isolated habitat patches are not a random sample from the metapopulation, rather they are more dispersive than females in old well-connected populations. High dispersal rate is heritable and is related to high flight metabolic rate and particular genotypes in the glycolytic enzyme locus PGI. As other life-history traits, such as body size, fecundity, and lifespan may be related to dispersal rate, it is important to examine the full set of correlated traits for their evolutionary and ecological consequences. Here we report on experiments conducted in a large (30 x 30 x 3 m) outdoor population cage built upon a natural habitat patch. Individuals for the experiments were sampled from newly-established and old populations within a large metapopulation, where the age, size, and spatial connectivity of populations are known. Results show that among-individual and among-population variation in dispersal rate is correlated with the reproductive performance of females, though there is no evidence for a trade-off between dispersal and fecundity. Preliminary results suggest that highly dispersive individuals with high flight metabolic rate have a shorter lifespan than less dispersive individuals. These results suggest that phenotype-dependent dispersal rate correlates with other life history traits in the Glanville fritillary. The rapid turnover of local populations (extinctions and re-colonisations) is likely to maintain phenotypic variation at the metapopulation level.

22-05 Talk

HABITAT CHOICE, PHENOTYPE–DEPENDENT DISPERSAL AND PARALLEL EVOLUTION IN A FRESHWATER ISOPOD.

Fabrice Eroukhmanoff [1], Anders Hargeby [2], Kristina Karlsson [1], Nina Nowshiravani [3], Erik Svensson [1]

[1] *Lund University, Animal Ecology, Lund Univeristy Box 117, 22100, Lund, Sweden*
[2] *Linköping Univeristy, Limnology, Linköping, Sweden*
[3] *Santa Cruz University, Animal Ecology, Santa Cruz, USA*

Fabrice.eroukhmanoff@zooekol.lu.se

The freshwater isopod *Asellus aquaticus* (Crustacea) inhabits many lakes of southern Sweden, among them Lake Tåkern and Lake Krankesjön. In these two lakes, shifts from phytoplankton to the macrophyte state have taken place in parallel during the last 20 years. Colonization and local adaptation to a new submerged vegetation habitat developed during a very short time period of only a few isopod generations and resulted in rapid evolution of habitat-specific colouration and body size.

Coloration and body size differ between two different habitats and two different ecotypes occur in both lakes : light pigmented and small isopods occur more frequently in stands of submerged vegetation dominated by stoneworts (*Chara* spp.) and dark pigmented and large isopods predominate nearby stands of reed (*Phragmites australis*), which is the ancestral habitat. These phenotypic differences are correlated with differences in local predation pressures and the general colouration of the environment.

We will present results showing that this rapid case of evolutionary diversification is promoted by low dispersal abilities, strong habitat preference for the native environment and partial sexual isolation which will all restrain gene flow between populations.

22-06 Talk

INFLUENCE OF PAST AND PRESENT ENVIRONMENTS ON NATAL DISPERSAL BEHAVIOUR IN SMALL MAMMALS

Jean-François Le Galliard [1]

[1] *CNRS, UMR 7625, Université Pierre et Marie Curie, 7 Quai St Bernard, 75005, Paris, France*

galliard@biologie.ens.fr

In many species, natal dispersal behaviour might depend on context-dependent intergenerational effects where conditions experienced when parents invest in their offspring influence the plasticity in natal dispersal after independence. Context-dependent intergenerational effects may be mediated by long-lasting impacts of parental environment on offspring morphology or behaviour. For example, parents living in high-quality territories may produce larger and more aggressive offspring that are better at settling in high-quality territories. In this talk, I review evidences for condition-dependence in natal dispersal behaviour from *Arvicolinae* rodents (voles, lemmings, muskrats). I also present the results of an experimental study using allometric and habitat engineering to test for context-dependent intergenerational effects on the natal dispersal behaviour of root voles (*Microtus oeconomus*). The conclusions of the review and this experiment are discussed in light with habitat choice theory.

22-07 Talk

SOCIAL PERSONALITIES INFLUENCE NATAL DISPERSAL AND FITNESS OUTCOMES IN COMMON LIZARD (LACERTA VIVIPARA)

Julien Cote [1], Jean Clobert [2]

[1] *Université de Bourgogne, Biogéosciences UMR CNRS 5561, 7 bd Gabriel, 21000, Dijon, France*
[2] *Station d'Ecologie Expérimentale du CNRS, USR 2936, Moulis, 09200, Saint-Girons, France*

jcote@snv.jussieu.fr

Animal personalities are common across taxa, and have important evolutionary and ecological implications. Such consistent individual differences correlate with important life history traits such as dispersal, survival and reproduction. Some environmental conditions are supposed to determine dispersers with a specific personality. Therefore, we hypothesized that dispersers from high-density populations should primarily be asocial individuals, whereas dispersers from low-density populations should be social individuals. In the common lizard (*Lacerta vivipara*), we measured attraction towards the odour of conspecifics on juveniles at birth as a metric of social tolerance. We then released these juveniles into populations of different densities and measured dispersal, subsequent survival and reproduction with regard to social tolerance. The social tolerance, constant across time, strongly reflects the individual dispersal and survival patterns with respect to population density. These results strongly suggest that social personalities exist and influence dispersal decisions, habitat selection and fitness outcomes. Further studies will help elucidate the proximate and ultimate determinants of social personalities.

22-01 Poster

GENETIC DIFFERENTIATION AT A SMALL GEOGRAPHIC SCALE IN THE PERCH (PERCA FLUVIATILIS L.)

Sara M. Bergek [1]

[1] *Uppsala University, Evolutionary Biology Centre (EBC), Dept of Animal Ecology, Norbyvägen 18D, 75236, Uppsala, Sweden*

sara.bergek@ebc.uu.se

Gene flow between coexisting or nearby populations normally prevents genetic divergence and local adaptation. Despite this, there are an increasing number of reports of sympatric sister-taxa, indicating potential divergence and speciation in the face of gene flow. A large number of such reported cases involve lake-dwelling fish, which are expected to run into few physical barriers to dispersal within their aquatic habitat. However, such cases may not necessarily reflect sympatric speciation if cryptic dispersal or behavioural barriers are common in lakes and other aquatic systems. In this study, we examined genetic differentiation in perch (*Perca fluviatilis* L.) from nine locations in a single, small lake (24 km^2), using microsatellites. We detected significant genetic differentiation in all but two pairwise comparisons. These patterns were not consistent with divergence-by-distance or the existence of kin-groups. Instead, they suggest that cryptic barriers to dispersal exist within the lake, allowing small-scale genetic divergence. Such an observation suggests that allopatric (or parapatric) divergence may be possible, even in small, apparently homogenous environments such as lakes. This has important consequences for how we currently view evidence from nature for sympatric speciation.

22-02 Poster

EVOLUTION OF MANDIBLE SHAPE IN WILD HOUSE MICE

Louis Boell [1], Diethard Tautz [1]

[1] *University of Cologne, Department of Genetics, Germany, Cologne, Zülpicher Str. 47, D-50674*

lboell@hotmail.de

Geometric morphometrics is used to compare mandible shape between different populations of wild house mice and to describe ontogeny and phenotypic plasticity of shape in captivity. First results include findings about differences between mice from France and from Iran. These will lead to the formulation of hypotheses about evolution and evolvability of mandible shape in the wild. These hypotheses will be tested by artificial selection experiments using microCT, and it is planned to map genetic factors correlated with shape differences in these experiments.

22-03 Poster

THE EVOLUTION OF SOCIAL INTERACTIONS IN A PROTIST: DISPERSAL AND INFORMATION USE IN TETRAHYMENA THERMOPHILA

Thierry Polard [1], Alexis S. Chaine [1], Jean Clobert [1]

[1] *Station d'Ecologie Experimentale du CNRS, Evolution et Diversite Biologique, Station du CNRS a Moulis, 09800, Moulis, France*

alexis.chaine@lsm.cnrs.fr

Recent studies have demonstrated maternal influence on dispersal strategies suggesting that a key life history trait may depend on social context. While plasticity in dispersal decisions has now been well documented, some species also show genetic variation in basic dispersal rates. We examined the role of social information in modifying dispersal rates in a unicellular protist that shows genetic variation for baseline dispersal strategies. We conducted a number of experiments to investigate how individuals use information regarding their social group to alter their dispersal decision. First, we investigated how information about the average population relatedness and similarity in social strategy (propensity to aggregate) affect dispersal decisions to understand one aspect of the evolution of social aggregation and plasticity in dispersal strategy. Second, we investigated how social species use cues from conspecifics as indirect information about their habitat and surrounding the populations to modify their dispersal strategy. Such experiments add to the growing view that behavior, social information, and plasticity play an important role in modifying classic life history traits including dispersal and sociality and highlight their importance in even the simplest organisms.

22-04 Poster

DOES SPATIAL CLUSTERING OF KIN EXPLAIN SEX-BIASED NATAL DISPERSAL?

Cas Eikenaar [1], Lyanne Brouwer [1], Jan Komdeur [1], David S. Richardson [2]

[1] *University of Groningen, Animal Ecology, Kerklaan 30, 9750 AA, Haren, Netherlands*
[2] *University of East Anglia, Centre for ecology, evolution and conservation, NR4 7TJ, Norwich, UK*

c.eikenaar@rug.nl

Sex-biased natal dispersal has often been explained as a mechanism of inbreeding avoidance. However, in many species natal dispersal distances (NDD) are short and tend to overlap between the sexes, which may set the stage for matings between relatives. To answer the question if sex biased natal dispersal functions to avoid inbreeding we need to know if the difference in NDD between the sexes is sufficient to effectively avoid matings between close relatives. In the Seychelles warbler, *Acrocephalus sechellensis,* a species with female-biased NDD, the sex difference in the chance of mating with a close relative is largest in adjacent territories. Females dispersing into adjacent territories could pair with close kin, because EPP levels are high and sires are often from adjacent territories. Males dispersing into adjacent territories have a very small chance of pairing with a close relative, because of the absence of intra-specific brood parasitism. In this paper, we assess whether the female bias in NDD is related to a sex difference in the distribution of kin around the dispersers' natal territories. We detect this distribution by calculating pairwise relatedness values between dispersers and all opposite sex breeders in the population at each possible dispersal distance. Furthermore, we experimentally give young males and females the opportunity to pair with breeders in adjacent territories. If the female-bias in NDD in the Seychelles warblers functions to avoid inbreeding, we expect females to ignore and males to occupy these vacancies.

22-05 Poster

HERITABILITY OF NATAL DISPERSAL IN SIBERIAN JAYS

Phillip Gienapp [1], Bo-Göran Lillandt [1], Juha Merilä [1]

[1] *University of Helsinki, Dept of Biol and Env Sciences, Viikinkaari 1 (PL 65), 00014, Helsinki, Finland*

phillip.gienapp@helsinki.fi

Dispersal behaviour can have important ecological and evolutionary consequences. Dispersing individuals can, for instance, found new populations, affect population dynamics of already existing populations, or prevent inbreeding depression, but also local adaptation. While evidence is accumulating that dispersal behaviour is phenotype dependent it is less clear whether it also has a genetic basis as the number of studies that probed directly into the genetics of dispersal behaviour is still limited. A heritable component of dispersal behaviour obviously could have strong evolutionary consequences. Studying dispersal behaviour in the wild is however hampered by that fact that study areas are limited. This means that, e.g., dispersal distances are necessarily biased since long distances are less likely observed than short distances. We analysed natal dispersal behaviour in a Finnish long-term study population of Siberian jays (*Perisoreus infaustus*). These long-lived birds normally disperse once and then maintain the same territory throughout their live. The study population has been followed since 1974 and all individuals have been genotyped with microsatellite markers enabling us to establish parentages and to construct a pedigree. We corrected the observed dispersal distances, which are necessarily biased, using a simulation model. Subsequently, we explored what role genetic and non-genetic factors, as rank in the family size hierarchy, play in determining natal dispersal in this bird species.

22-06 Poster

EFFECT OF SOCIAL ENVIRONMENT ON POST FLEDGLING MOVEMENTS IN THE GREAT TIT (PARUS MAJOR): A NEW APPLICATION FOR TRANSPONDERS IN SMALL PASSERINES

Marion Nicolaus [1], Karen M. Bouwman [1], Stephanie P. M. Michler [1], Richard Ubels [1], Marco Van der Velde [1], Christiaan Both [1], Niels J. Dingemanse [1], Joost M. Tinbergen [1]

[1] *University of Groningen, Animal Ecology, PO box 14, 9750 AA Haren, The Netherlands*

m.nicolaus@rug.nl

Dispersal and habitat selection are important factors that influence individual fitness. Multiple mechanisms could shape the evolution of these factors. Dispersal and settlement decisions can be affected by frequency dependent effects caused by competition as well as by the use of public information on habitat quality. We study here the effects of competition within and between sexes and of the use of public information on individual decisions by manipulating the fledgling density and sex ratio of 12 woodlots. If competition avoidance is the main mechanism behind post fledgling dispersal decisions, we expect fledglings to disperse further away from high density and male biased plots where intraspecific competition is expected to be higher. However, if birds use public information for their dispersal decisions, we expect birds to stay more in high density and male biased plots that potentially indicate good quality habitats. To test these hypotheses, 396 nestlings (194 females, 202 males) were subcutaneously implanted with a transponder and 304 breeding adults were equipped with an external transponder on their ring in 2006. Between August and December 2006, 24 feeding tables were placed in the study area in order to collect continuous and automated data of the bird visits. We then quantified the effects of the birds social environment (plot density and plot sex ratio) on post fledgling dispersal distances and on the chance of being recorded on a feeder. We found no effect of social environment on the chance of visiting a feeder. However, plot sex ratio had a sex specific effect on post fledgling movements, females dispersing further away when plot sex ratio increased. These results suggest that inter-sexual competition could be the mechanism behind post fledgling movements.

22-07 Poster

GENETIC CONTRIBUTION OF EXPERIMENTALLY INTRODUCED INDIVIDUALS IN A NATURAL HOUSE SPARROW META POPULATION.

Sigrun Skjelseth [1], Henrik Jensen [1], Thor Harald Ringsby [1], Bernt-Erik Sæther [1]

[1] *NTNU, Deptartment of biology, Høgskoleringen 5, N- 7419, Trondheim, Norway*

sigrun.skjelseth@bio.ntnu.no

The introduction of alien species and individuals of deviant genotypes into wild populations is one of the major threats towards global biodiversity. On the other hand, introductions may also be an important management tool in the conservation of threatened or vulnerable populations.

An important issue concerning this is the potential that the introduced individuals spread and interfere both demographically and genetically with the local population. We conducted a large scale experiment where we introduced 123 house sparrows from a distant population into 18 local populations without changing population density or sex ratio. We have previously shown that introduced individuals disperse more frequently and over longer distances than residents. In addition, we have demonstrated that the distribution and frequency of dispersal of introduced individuals may be predicted by their sex as well as by phenotypic characteristics. The degree of influence that introduced individuals constitute genetically to a local population is however determined by the contribution of offspring to future generations. In genetic restoration programs and re-introductions reproduction among such individuals are of vital importance for success. On the basis of constructed pedigrees, we here examine the relative reproductive rates and survival of introduced individuals and residents. Our aim is to increase our understanding of factors that affect the rate of spread of alien genotypes and alleles.

22-08 Poster

INTRASPECIFIC COMPETITION DRIVES INCREASED RESOURCE USE DIVERSITY WITHIN A NATURAL POPULATION

Richard Svanbäck [1], Daniel I. Bolnick [2]

[1] *Uppsala University, Dept. of Ecology and Evolution, Husargatan 3, 75123, Uppsala, Sweden*
[2] *University of Texas at Austin, Section of Integrative Biology, 1 University Station C0930, 78712-0253, Austin, USA*

richard.svanback@ebc.uu.se

Resource competition is thought to play a major role in driving evolutionary diversification. For instance, in ecological character displacement, coexisting species evolve to use different resources, reducing the effects of interspecific competition. It is thought that a similar diversifying effect might occur in response to competition among members of a single species. Individuals may mitigate the effects of intraspecific competition by switching to use alternative resources not used by conspecific competitors. This diversification is the driving force in some models of sympatric speciation, but has not been demonstrated in natural populations. Here, we present experimental evidence confirming that competition drives ecological diversification within natural populations. We manipulated population density of three-spine stickleback (*Gasterosteus aculeatus*) in enclosures in a natural lake. Increased population density led to reduced prey availability, causing individuals to add alternative prey types to their diet. Because phenotypically different individuals added different alternative prey, diet variation among individuals increased relative to low-density control enclosures. Competition also increased the diet-morphology correlations, so that the frequency-dependent interactions were stronger in high competition. These results confirm that resource competition promotes niche variation within populations, but also show that this increased diversity can arise via behavioural plasticity alone, without the evolutionary changes commonly assumed by theory.

22-09 Poster

MOLECULAR INSIGHTS INTO PHENOTYPE DEPENDENT DISPERSAL AND FITNESS CONSEQUENCES IN THE WILD USING CANDIDATE GENES.

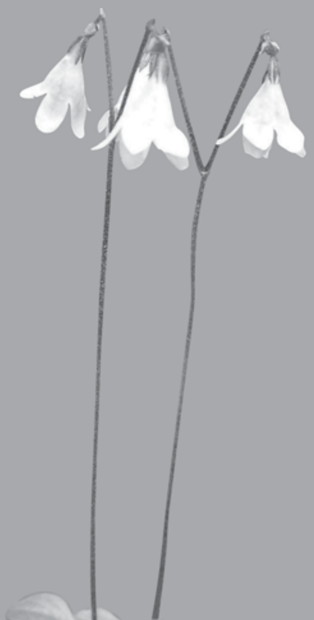
Christopher W. Wheat [1], Jim Marden [2], Ilkka Hanski [1]

[1] *University of Helsinki, Dept. of Env. & Bio. Sci., Viikinkaari 1, PO Box 65, 00014, Helsinki, FINLAND*
[2] *Penn State University, Biology, 16802, State College, PA, USA*

cww10@psu.edu

I begin with an overview of some recent findings from our group regaring the genetics of dispersal in a metapopulation of the Glanville fritillary (Melitaea cinxia) butterfly. Studies have documented a genetic basis for dispersal differences that manifest themselves at the phenotypic level in terms of dispersal distance and metabolic rate. Recent work has also demonstrated that metabolic rate correlates very well with distance moved in the wild (over several km). Metabolic rate also correlates with genetic variation at the phosphoglucose isomerase (Pgi) gene, whose variation is non-randomly distributed among local populations in this metapopulation. Pgi genotype has also been found to correlate with local population growth rate, which is a powerful measure of realized fitness in the wild. Molecular study of the Pgi gene region reveals a strong signature of balancing selection, suggesting that the reported correlations do have realized fitness consequences that have been operating over evolutionary time. In individual butterflies, Pgi appears to be interacting with plastic variation in a flight muscle protein, Troponin-t (Tnt). Tnt is alternatively spliced, with relative amounts of different splice forms associated with flight muscle performance. Relative abundance of Tnt alternative transcripts change with insect age and mating, suggesting a possible mechanism that could affect post mating dispersal. The implications of these studies for assessing the match between phenotype and habitat are discussed.

Gene mapping in natural populations



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Wednesday August 22 *Location*: Ekonomikum 1

Symposium 23: Gene mapping in natural populations

ORGANIZERS: Jon Slate, University of Sheffield, UK
Christian Lexer, Royal Botanic Gardens, Kew

09.45-10.15	**Loren Rieseberg** (invited) QTL and Association Mapping in Wild and Domesticated Sunflowers
10.15-10.45	**Hopi Hoekstra** (invited) Finding the genes that contribute to adaptive variation in natural populations of mice
10.45-11.05	**Katri Kärkkäinen** Genes and alleles causing adaptive variation in trichome production in natural populations of Arabidopsis lyrata
11.05-11.35	*Coffee*
11.35-11.55	**David Hall** Mapping variation in candidate genes for phenology along a latitudinal gradient in European Aspen
11.55-12.15	**Alex Buerkle** Methods and models for admixture mapping in populations of hybrids
12.15-12.35	**Tiffany Malek** Admixture mapping of male nuptial colour in a nascent hybrid population of threespine sticklebacks
12.35-14.00	*Lunch, council*
14.00-14.30	**Bengt Hansson** (invited) Linkage mapping, linkage disequilibrium and heterozygosity-fitness correlations in a passerine bird, the great reed warbler
14.30-14.50	**Niclas Backström** Gene mapping in a wild bird population
14.50-15.10	**Jake Gratten** Genetic variation in natural populations: linkage mapping of fitness related traits in Soay sheep
15.10-15.30	**Lena Wilfert** Natural variation in the genetic architecture of host resistance in the bumblebee Bombus terrestris
15.30-16.00	*Coffee*
16.00-16.20	**Anti Vasemägi** QTL mapping of ecologically relevant early life-history traits in Atlantic salmon
16.20-16.40	**Luisa Orsini** Fitness consequences of single nucleotide polymorphism at the Pgi locus in the Glanville fritillary butterfly
16.40-17.00	**Kees van Oers** Drd4 gene polymorphisms are associated with personality variation in a passerine bird
17.00-17.20	**Nolan Kane** Molecular evolution across the Asteraceae: micro- and macroevolutionary processes

23-01 Talk

QTL AND ASSOCIATION MAPPING IN WILD AND DOMESTICATED SUNFLOWERS

Loren H. Rieseberg [1]

[1] *University of British Columba, Botany, 3529-6270 University Blvd, V6T 1Z4, Vancouver, Canada*

lriesebe@interchange.ubc.ca

Advances in genetic mapping methodologies make it feasible to localize QTLs that contribute to adaptation and speciation. However, it has not been possible to employ these methods in many wild species because of difficulties associated with creating and propagating recombinant populations of sufficient size for QTL analyses. Genetic mapping in natural populations offers a potential solution to these problems. If candidate genes are unknown and dense marker maps are unavailable, hybrid zones or admixed populations provide a means for identifying QTLs of interest. On the other hand, if good candidate genes are available, then natural populations with low LD can be employed to associate sequence or expression variation with phenotypic variation. Here, we explore both approaches in wild and domesticated sunflowers. We have analyzed hybrid zones between two pairs of wild sunflower species, H. annuus × H. petiolaris and H. annuus × H. bolanderi, and association analyses are underway for a panel of 96 wild and domesticated sunflower genotypes × 100 candidate genes. Results from our hybrid zone work indicate that while mapping in hybrid zones presents many challenges, access to highly recombinant individuals can increase mapping precision, as well as the number of QTLs detected for traits underlying reproductive isolation.

23-02 Talk

FINDING THE GENES THAT CONTRIBUTE TO ADAPTIVE VARIATION IN NATURAL POPULATIONS OF MICE

Hopi E. Hoekstra [1]

[1] *Harvard University, Department of Organismic and Evolutionary Biology and The Museum of Comparative Zoology, Cambridge, MA 02138, USA*

hoekstra@oeb.harvard.edu

Ecological genetics has entered the genomic era, with one of its main goals the identification of genes underlying ecologically important traits. In this talk I discuss several ways to connect genotype to phenotype in non-model systems. I illustrate these approaches using natural populations of mice (genus *Peromyscus*) that have recently colonized novel habitats. In several cases, mice have invaded sandy habitats (including barrier islands and mainland sand dunes), and have quickly evolved many new traits relative to their ancestral counterparts, including novel pigmentation, longer tails, larger feet, and unique burrowing behavior. I discuss how we are working to identify the genetic regions, genes and mutations responsible for these adaptations, and then describe how this approach can be extended to other traits (both morphological and behavioral) and other species. Finally, I will examine the question of what having "the genes in hand" can really tell us about ecology and adaptation in nature.

23-03 Talk

GENES AND ALLELES CAUSING ADAPTIVE VARIATION IN TRICHOME PRODUCTION IN NATURAL POPULATIONS OF ARABIDOPSIS LYRATA

Katri Kärkkäinen [1], Karolina Tandre [2], Helmi Kuittinen [3], Outi Savolainen [3], Jon Ågren [4]

[1] Finnish Forest Research Institute, Muhos Research Unit, Kirkkosaarentie 7, 91500, Muhos, Finland
[2] Uppsala University, Dept Evolution, Genomics and Systematics, EBC, Uppsala, Sweden
[3] University of Oulu, Department of Biology, Oulu, Finland
[4] Uppsala University, Department of Ecology and Evolution, Uppsala, Sweden

katri.karkkainen@metla.fi

We examined the genes and alleles governing variation in trichome production in natural populations of the perennial, outcrossing herb Arabidopsis lyrata, and studied the effects of these alleles on resistance to herbivory and on plant fecundity in the wild. An association study in three Swedish populations of A. lyrata suggested that allelic variation in the candidate gene GLABROUS1 can explain most of the polymorphism in trichome production (glabrous vs. trichome-producing plants). Transformation studies confirmed that a non-synonymous substitution in a highly conserved myb-region of the gene causes glabrousness. Other mutations in the same gene were found to be the most likely cause of glabrousness in other natural populations of A. lyrata and A. thaliana. A QTL-study revealed another gene affecting the trait, and showed allele-specific interactions between the two genes. Phenotypic and functional effects of the most important QTN were studied in a natural population of A. lyrata. Trichome production may serve as an important model when evolution of more complex traits is being assessed.

23-04 Talk

MAPPING VARIATION IN CANDIDATE GENES FOR PHENOLOGY ALONG A LATITUDINAL GRADIENT IN EUROPEAN ASPEN

David Hall [1], Stefan Jansson [2], Pär K. Ingvarsson [1]

[1] Umeå University, Ecology and environmental Science, 90187, Umeå, Sweden
[2] Umeå University, Umeå Plant Science Centre, Department of Plant Physiology, 90187, Umeå, Sweden

david.hall@emg.umu.se

Correct timing of yearly occurring events is crucial to fitness. Onset of growth and initiation of winter dormancy are classical examples of a trade-offs between competition and survival in perennial plants. The aim was to study the genetic basis of variation in phenology in *Populus tremula* across a latitudinal gradient in Sweden. We sampled 12 natural populations extending over 10 latitudinal degrees and scored several phenology traits in two common gardens. We also scored sequence variation in 10 candidate genes from the photoperiodic pathway. Sequence variants found in a few of these genes show associations with variation in phenology and explain a sizable fraction of the natural variation in phenology. There are no indications that these genes have genetic differentiation that exceeds genetic differentiation at neutral markers. These results confirm theoretical studies on differentiation of QTLs underlying continuous traits, where divergent selection creates co-variance between QTLs underlying phenotypic traits, resulting in large phenotypic shifts even with little genetic differentiation at individual QTLs.

23-05 Talk

METHODS AND MODELS FOR ADMIXTURE MAPPING IN POPULATIONS OF HYBRIDS

Alex Buerkle [1], Christian Lexer [2]

[1] University of Wyoming, Department of Botany, 1000 E. University Ave., 82071, Laramie, WY, USA
[2] Royal Botanic Gardens, Kew, Jodrell Laboratory, TW9 3DS, Surrey, UK

buerkle@uwyo.edu

Hybridization between species presents opportunities and challenges for mapping in natural populations. Admixed populations exhibit linkage disequilibrium between markers and genes of interest, which makes mapping feasible. Furthermore, in hybrid zones with backcrosses and later generation hybrids, linkage disequilibrium will decay and may allow mapping at a finer resolution than is possible in artificial crosses with only a few generations of recombination. As with other approaches to gene mapping in natural populations, a challenge is the lack of a known pedigree or ancestry of individuals. With hybrids we seek good estimates of individual admixture or ancestry across the genome and utilize these as an index of overall genomic composition. In our search for fitness-related genes in hybrid populations, we are interested in identifying genotypes at a locus that depart from this background genomic composition (e.g., "excess admixture"). We have developed statistical approaches to identify genotypes at a locus that are over- or underrepresented relative to expectations derived from different genetic models. For example, at a locus we might detect departures from a neutral model of introgression that might better fit a model of underdominance and selection against interspecific heterozygotes. The linear modeling approach can be extended to model phenotypic data, as well as incorporate environmental covariates. Thus, our approach represents an extension of two different concepts: that of ‘mapping through admixture linkage disequilibrium’ (MALD), and that of ‘population genomics’ work to detect the locus-specific signature of selection. These methods can be applied at the level of genome scans of variation at marker loci (e.g., anonymous or gene-based SSR) or to individual nucleotide polymorphisms. We will illustrate our approach with applications to our studies of introgression in European Populus species.

23-06 Talk

ADMIXTURE MAPPING OF MALE NUPTIAL COLOR IN A NASCENT HYBRID POPULATION OF THREESPINE STICKLEBACKS

Tiffany B. Malek [1], Janette W. Boughman [2], Catherine L. Peichel [3]

[1] University of Washington, Molecular & Cellular Biology, 1100 Fairview Ave N., 98109, Seattle, United States
[2] University of Wisconsin-Madison, Zoology, 1100 Fairview Ave N., 98109, Madison, United States
[3] Fred Hutchinson Cancer Research Center, Human Biology, 1100 Fairview Ave N., 98109, Seattle, United States

tmalek@u.washington.edu

To address the genetic basis of adaptation, we study divergence in nuptial coloration in the threespine stickleback (Gasterosteus aculeatus). In most populations, male sticklebacks display a bright red throat and blue eyes during the breeding season, and this color plays an important role in mate choice and species recognition. However, some stickleback populations have evolved black nuptial color in response to differences in water coloration. This divergence in male nuptial color has been shown to contribute to reproductive isolation between sympatric stickleback populations. To identify the genomic regions responsible for this change in male color, we are developing an admixture mapping approach using a recently formed hybrid population of threespine stickleback found in Enos Lake (British Columbia, Canada). Recent genetic and morphological data suggest that two once reproductively isolated populations have been interbreeding for the last 10 to 20 generations. In a preliminary genome scan (576 markers on 224 individuals), we have identified at least one region of the genome associated with male nuptial color in this natural hybrid population. Currently, we are performing a more extensive genome scan with denser marker coverage (1 marker per 500 kb) and an increased number of individuals (n=500). This admixture mapping approach complements quantitative trait locus (QTL) mapping that we have performed using fish from the same location. Paired with our QTL findings, this work will provide important insights into the genetic basis of adaptation and speciation and provide the basis for the eventual identification of the actual genes that contribute to variation in male nuptial color.

23-07 Talk

LINKAGE MAPPING, LINKAGE DISEQUILIBRIUM AND HETEROZYGOSITY-FITNESS CORRELATIONS IN A PASSERINE BIRD, THE GREAT REED WARBLER

Bengt Hansson [1]

[1] *Lund University, Department of Ecology, Ecology Building, 22362, Lund, Sweden*

bengt.hansson@zooekol.lu.se

Genome structure has been found to be highly conserved between distantly related birds and recent data suggest that this is true also for gene order within chromosomes. I present comparative linkage mapping data confirming that synteny is maintained for large chromosomal regions in chicken and a passerine bird, the great reed warbler (*Acrocephalus arundinaceus*), with the exception of two large inversions. In contrast, the linkage map distances in great reed warblers were only 6 and 13% of those in chickens for males and females, respectively. This very low recombination rate in great reed warblers is interesting in light of (i) the high level of linkage disequilibrium in our Swedish study population, a level comparable to that detected in some extremely bottlenecked populations, and (ii) the previously detected association between marker-based heterozygosity and variation in fitness-associated traits in the species.

23-08 Talk

GENE MAPPING IN A WILD BIRD POPULATION

Niclas Backstrom [1], Hans Ellegren [1]

[1] *Uppsala University, Dept of Evolutionary Biology, Uppsala, Sweden*

Niclas.Backstrom@ebc.uu.se

There is a current interest in combining knowledge from the fields of genomics and evolutionary biology, for example, in tracing the associations between genetic components and phenotypic traits in natural populations. If we can start to unveil the links between genotypes and phenotypes, this would clearly increase our knowledge of fundamental evolutionary processes, for example natural selection in wild populations, reproductive isolation or speciation. Birds are useful study organisms in this respect, because there is ample background information on many general aspects of ecology and evolutionary biology, such as mate choice, sexual selection, life history evolution and speciation. However, at present, there is very limited information on the genomic biology of wild bird species. Now we have exploited the chicken genome sequence to develop a genome wide set of more than 250 evenly distributed and conserved avian reference gene markers. We test these markers for their usefulness in other bird species and provide examples of their application in sequence analysis of a non-model genome, large-scale screening for single nucleotide polymorphisms (SNPs) and a multi-gene approach to avian phylogenetics. In addition, developed polymorphic markers are used in an attempt to create a genome-wide linkage map of one of the most important model species in avian ecological and evolutionary research, the collared flycatcher.

23-09 Talk

GENETIC VARIATION IN NATURAL POPULATIONS: LINKAGE MAPPING OF FITNESS RELATED TRAITS IN SOAY SHEEP

Dario Beraldi [1], Jacob Gratten [2], Allan F. McRae [3], Peter M. Visscher [3], Jon Slate [2], Josephine M. Pemberton [1]

[1] *University of Edinburgh, Institute of Evolutionary Biology, King's Buildings, EH9 3JT, Edinburgh, UK*
[2] *University of Sheffield, Animal & Plant Sciences, Western Bank, S10 2TN, Sheffield, UK*
[3] *Queensland Institute of Medical Research, Genetic Epidemiology, Royal Brisbane Hospital, Brisbane 4029, Brisbane, Australia*

j.slate@sheffield.ac.uk

Traits under the pressure of natural selection are expected to lose their genetic variability since the negative genetic variants are counter-selected and replaced by the positive alleles. However, direct, empirical observations show that fitness related traits maintain, or even enhance, their genetic variability in the face of selection. One strategy by which the complexity of continuous characters can be dissected, and the loci that contribute to trait variation identified is linkage mapping. A long-term study of the Soay sheep on St Kilda, offers an unprecedented opportunity to dissect the architecture of fitness related traits in the wild. A pedigree of 588 animals was genotyped to build a complete genetic map and a whole genome scan was carried out to detect loci for qualitative and quantitative traits related to fitness. The loci affecting horn type and two aspects of coat colour were mapped: *Horn type* mapped to chromosome 10, *Coat colour* to chromosome 2, *Coat pattern* to chromosome 13 (LOD scores >3). One genomic region showed significant linkage with the variation in jaw length (chromosome 11, LOD= 3.59). In addition, suggestive linkages were detected for hind leg length (chromosome 15, LOD= 2.89), birth weight (chromosome 8, LOD= 2.54), and timing of birth (chromosome 2, LOD= 2.70). Finally, two suggestive linkages were scored for resistance to the gastrointestinal parasite coccidia (chromosome 3 and X, LOD= 2.68 and 2.21, respectively). The results reported here will improve our understanding of the evolution and genetics of natural populations by allowing a more realistic modelling of the study traits, and by opening the way towards the molecular characterisation of the genomic regions of interest.

23-10 Talk

NATURAL VARIATION IN THE GENETIC ARCHITECTURE OF HOST RESISTANCE IN THE BUMBLEBEE BOMBUS TERRESTRIS

Lena Wilfert [1], Juergen Gadau [2], Paul Schmid-Hempel [1]

[1] *ETH Zürich, IBZ, Universitätsstrasse 16, 8092, Zürich, Switzerland*
[2] *Arizona State University, School of Life Sciences, AZ 85287-4501, Tempe, USA*

lena.wilfert@env.ethz.ch

The genetic architecture of fitness-relevant traits in natural populations is a topic that has remained almost untouched by quantitative genetics. Given the importance of parasitism for the host's fitness, we used QTL mapping to study the genetic architecture of traits relevant for host-parasite interactions in the trypanosome parasite, Crithidia bombi and its host, Bombus terrestris. The three traits analyzed were the parasite's infection intensity, the strength of the general immune response (measured as the encapsulation of a novel antigen) and body size. The genetic architecture of these traits was examined in three natural, un-manipulated mapping populations of B. terrestris. Our results indicate that the intra-colonial phenotypic variation of all three traits is based on a network of QTLs and epistatic interactions. While these networks are similar between mapping populations in complexity and number of QTLs as well as in their epistatic interactions, the variability in the position of QTL and the interacting loci was high. Only one QTL for body size was plausibly found in at least two populations. QTLs for encapsulation and Crithidia infection intensity were located on the same linkage groups.

23-11 Talk

QTL MAPPING OF ECOLOGICALLY RELEVANT EARLY LIFE-HISTORY TRAITS IN ATLANTIC SALMON

Anti Vasemägi [1], Craig R. Primmer [1]

[1] *University of Turku, Department of Biology, Vesilinnantie 5, 20014, Turku, Finland*

anti.vasemagi@utu.fi

Understanding the genetic basis of phenotypic variation in natural populations represents one of the most challenging tasks in evolutionary biology. Despite the popularity of quantitative trait locus (QTL) mapping approaches in genetic model organisms and agricultural species, the progress in finding QTLs linked to ecologically relevant traits has been relatively limited. Here, we present the results of QTL mapping of ecologically relevant early life-history traits in full-sib families from an outbred Atlantic salmon (*Salmo salar* L.) population. We describe the genetic architecture of two traits (time of emergence from the gravel and length of the fry) that are expected to have major fitness consequences in natural environments. Taking advantage of limited recombination in salmonid males, the initial mapping focused on identification of large chromosomal regions containing QTLs from the paternal side. Further fine-scale QTL mapping was then performed using the females as a segregating parent. We discuss the prospects of finding fitness related QTLs with major effect in the wild and compare the identified QTLs with similar traits in rainbow trout (*Oncorhynchus mykiss*). The present study demonstrates the challenges of detecting standing variation in a long-lived outbred natural population and represents a first step towards identification of ecologically relevant functional variation in salmon.

23-12 Talk

FITNESS CONSEQUENCES OF SINGLE NUCLEOTIDE POLYMORPHISM AT THE PGI LOCUS IN THE GLANVILLE FRITILLARY BUTTERFLY

Luisa Orsini [1], Christopher W. Wheat [1, 2], Jouni Kvist [1, 3], Mikko Frilander [3], Ilkka Hanski [1]

[1] *University of Helsinki, Department of Biological and Environmental Sciences, PO Box 65 (Viikinkaari 1), 00014, Helsinki, Finland*
[2] *Penn State University, Department of Biology, University Park, PA, 16802, USA*
[3] *University of Helsinki, Institute of Biotechnology, P.O.Box 56 (Viikinkaari 9), 00014, Helsinki, Finland*

luisa.orsini@helsinki.fi

The phosphoglucose isomerase (*Pgi*) encodes a key enzyme of glucose metabolism and thus plays a role in the supply of energy (ATP) to flight muscles in insects. *Pgi* is known to have major effects on fitness in a wide range of taxa, and past studies on the Glanville fritillary butterfly (*Melitaea cinxia*) have shown that allozyme variation at PGI is associated with variation in flight metabolic rate and dispersal rate in the wild. Furthermore, allelic variation in *Pgi* affects population growth and hence has direct consequences for population dynamics. We have sequenced the *Pgi* gene in the Glanville fritillary and identified the segregating amino acid sites; two of the sites were charge-changing amino acids known to have potential functional consequences in *Colias* butterflies. Targeting three charge-changing amino acid sites, we designed specific SNP primers that discriminate among the main allozymes and validated the SNPs by sequencing tens of individuals. Using SNPs we reanalyzed three independent datasets (n=1000), previously analyzed with allozyme electrophoresis. We show that one of the SNPs explains phenotypic variation in flight metabolic rate, dispersal rate, and population growth in the Glanville fritillary. These results confirm the ones previously obtained with allozymes, but most importantly provide a high throughput for the screening of wild populations for fitness effects of *Pgi*.

23-13 Talk

DRD4 GENE POLYMORPHISMS ARE ASSOCIATED WITH PERSONALITY VARIATION IN A PASSERINE BIRD

Kees Van Oers [1], Andrew E. Fidler [2], Pieter J. Drent [1], Sylvia Kuhn [3], Jacob C. Mueller [3], Bart Kempenaers [3]

[1] *Netherlands Institute of Ecology, Animal Population Biology, PO Box 40, 6666 ZG, Heteren, Netherlands*
[2] *Cawthron Institute, Private Bag 2, Nelson, New Zealand*
[3] *Max-Planck Institute for Ornithology, Behavioural Ecology and Evolutionary Genetics, PO Box 1564, 82319, Starnberg, Germany*

k.vanoers@nioo.knaw.nl

To better understand the ecological and evolutionary significance of personality variation in natural animal populations a greater understanding of the underlying molecular genetic mechanisms is needed. Polymorphisms in human dopamine receptor D4 gene (*Drd4*) variants have been associated with variation in personailty (novelty seeking behaviour). We investigated two *P. major Drd4* gene polymorphisms for evidence of association with novelty-seeking behaviour: a coding region single nucleotide polymorphism (SNP830) and a 15 bp indel (ID15). Frequencies of the SNP830 genotypes, but not the ID15 genotypes, differed significantly between two *P. major* lines selected for divergent levels of 'early exploratory behaviour' (EEB). We comfirmed this in free-living, unselected birds where we also found a significant association between SNP830 genotypes and differing mean EEB levels. This work heralds the possibility of following micro-evolutionary changes in frequencies of behaviourally relevant *Drd4* polymorphisms within populations where natural selection acts differentially on different personality types.

23-14 Talk

MOLECULAR EVOLUTION ACROSS THE ASTERACEAE: MICRO- AND MACROEVOLUTIONARY PROCESSES

Nolan C. Kane [1], Michael S. Barker [1], Loren H. Rieseberg [1]

[1] *Indiana University, Biology, 1001 E 3rd St., 47401, Bloomington, IN, USA*

nkane@interchange.ubc.ca

The Asteraceae (Compositae) is a large family of over 25,000 wild, weedy and domesticated species that compose approximately 10% of all angiosperms. It is also one of the most diverse flowering plant families with habits that include annual and perennial herbs to trees which exist in nearly every terrestial ecosystem. Through multiple radiations, members of the family have come to occupy every continent except Antarctica. Thus, the Asteraceae provide a unique opportunity to understand the evolutionary genomics of lineage radiation and diversification at numerous phylogenetic scales. Using a database of over 700,000 ESTs from 21 species representing four of the major lineages of the Asteraceae, we performed multiple bioinfomatic analyses to assess neutral and non-neutral evolutionary processes across this diverse plant family. Candidate genes under selection were identified in each species by calculating Ka/Ks, Likelihood Ratio Tests, and other statistics. Rates of evolution at silent and coding sites were assessed for different Gene Ontology functional categories, comparing rates of evolution over shorter and longer evolutionary time scales. Results indicate that macro- and micro-evolutionary processes share some similarities but in general are substantially different at the molecular evolutionary level. These analyses also point to particular classes of genes which may be crucial in shaping the radiation of this diverse plant family.

23-01 Poster

FUNCTIONAL AND STATISTICAL GENETIC EFFECTS IN NATURAL POPULATIONS.

José M. Álvarez-Castro [1], Arnaud Le Rouzic [1], Lars Rönnegård [1], Örjan Carlborg [1]

[1] *Uppsala University, Linnaeus Centre for Bioinformatics, Husargatan 3, BMC Box 598, 75124, Uppsala, Sweden*

jose.alvarez-castro@lcb.uu.se

The recent eruption of molecular techniques to delve into the genomes of all kinds of species entails a challenge for the development of theory to appropriately analyze the not long ago unconceivable sets of data that are now routinely generated. Here, we deal with functional and statistical models of genetic effects for studying natural populations.

We present the NOIA (Natural and Orthogonal InterActions) model, a new general framework for modeling genetic effects based on one functional and one statistical formulation. The functional formulation models natural effects of allele substitutions from reference individual genotypes, whereas the statistical formulation models average effects of allele substitutions over populations. The NOIA model successfully unifies statistical and functional modeling of genetic effects with arbitrary epistasis. This means, in particular, that functional models of epistasis, which until now have been used to study long-term evolution and effects of drift in adaptation with simulated data, can now be fed with real data from quantitative trait loci (QTL) experiments.

The statistical formulation of the NOIA model is orthogonal in situations where previous models of statistical epistasis are not. Therefore, NOIA is the most convenient model to estimate genetic effects, particularly in natural populations, which do not fulfill the idealized assumptions of the classical models for QTL analysis in experimental populations, like the F_2. To illustrate the advantages of NOIA, we implemented it for interval mapping using Haley-Knott regressions and applied it to both simulated and experimental data. We show how to translate and compare genetic effects obtained by QTL analysis in different populations, how to obtain functional genetic effects from statistical ones and how robust NOIA is to deviations from ideal situations assumed by previous models.

23-02 Poster

USING MICROARRAYS TO IDENTIFY RESISTANCE GENES IN NATURAL POPULATIONS OF HOUSE FINCHES

Camille Bonneaud [1], Susan Balenger [2], Geoffrey Hill [2], Scott V. Edwards [1]

[1] *Harvard University, Dep. of Organismic and Evolutionary Biology, 26 Oxford Street, 02138, Cambridge, U.S.A.*
[2] *Auburn University, Dep. of Biological Sciences, 331 Funchess Hall, 36849, Auburn, U.S.A.*

cbonneaud@oeb.harvard.edu

DNA microarrays have revolutionized our ability to measure genome-wide variation within and between natural populations. They allow us to estimate the quantitative variations in mRNA expression that are essential to adaptive evolution and that exist between treatments, populations and individuals. Furthermore, by highlighting differences in transcripts levels, they also pinpoint the genes that are likely to be under selection. One can then use those selected genes or their regulatory regions in population genetic analyses. Following on recent experiments using a less precise measure of gene expression, suppressive subtractive hybridization (SSH), we used a microarray to explore the genomic effects of an epizootic of *Mycoplasma gallisepticum* (hereafter referred as MG) on a wild vertebrate host, the House finch (*Carpodacus mexicanus*). The microarray was designed using cDNA clones from two SSH libraries that were found to be up and down-regulated in the spleen of MG-infected house finches. We hybridized the array using spleen samples from experimentally infected house finches originating from the eastern US population, which has been exposed to MG since 1994, and from the south-western US population, which has never encountered the pathogen. We then characterized the genes whose expressions are influenced by MG infection. We were also able to estimate the selective impact of MG exposure on host expression profiles by comparing the transcriptomes of eastern and south-western birds. We discuss the use of microarrays both to identify fitness-related genes and gene networks in non-model organisms for which there is little or no prior genomic information and to uncover evolution on genome-wide scales in natural populations.

23-03 Poster

EFFECT OF TWO INTERFERING SELECTIVE SWEEPS ON PATTERNS OF NEUTRAL POLYMORPHISM

Luis-Miguel Chevin [1], Sylvain Billiard [2], Frédéric Hospital [3]

[1] *CNRS, Génétique végétale, Ferme du Moulon, 91190, Gif-sur-Yvette, France*
[2] *Université Lille I, Génétique et Evolution des Populations végétales, Bâtiment SN2, 59655, Villeneuve d'Ascq, France*
[3] *INRA, Génétique végétale, Ferme du Moulon, 91190, Gif-sur-Yvette, France*

chevin@moulon.inra.fr

When a beneficial mutation goes to fixation, it temporarily decreases the surrounding neutral polymorphism due to the hitchhiking effect. Those selective sweeps have been widely used to detect recent targets of positive selection. We study the hitchhiking effect of two closely linked loci under positive selection. We show that it is not simply equivalent to the sum of individual hitchhikings, because the beneficial mutations also interfere with each other (Hill-Robertson effect). Depending on the location of the neutral locus, the effects of both hitchhikings are either antagonistic or synergetic, which leads to an asymmetry in the polymorphism pattern: there is paradoxically more diversity, and hence less power to reject the neutral hypothesis (using Tajima's D and Fay & Wu's H) for loci located between the selected mutations than for loci outside the interval. Our results shed light on empirical data from the sex-ratio distorting X chromosome in Drosophila simulans.

23-04 Poster

GENETICS OF INCIPIENT SPECIATION: G X E INTERACTIONS AND THE DETERMINANTS OF MATE RECOGNITION.

William J. Etges [1], Cassia C. De Oliveira [1], Mohamed A. Noor [2], Michael G. Ritchie [3]

[1] *University of Arkansas, Biological Sciences, SCEN 632, 72701, Fayetteville, United States*
[2] *Duke University, Biology Department, 27708, Durham, United States*
[3] *University of St. Andrews, School of Biology, KY16 9TS, St. Andrews, UK*

wetges@uark.edu

Fitness variation, mating success, cuticular hydrocarbon variation, and courtship songs were investigated in a 2-environment quantitative trait locus (QTL) analysis in diverging populations of Drosophila mojavensis. Baja California and mainland Mexico populations of D. mojavensis feed and breed on different host cacti, so these host plants were used to culture F2 males to examine host specific QTL effects and GxE interactions influencing development time, mating success, cuticular hydrocarbon profiles, and courtship songs. 21 microsatellite loci distributed across all 5 major chromosomes were used to co-localize effects of all traits.

Development time was influenced by multiple QTL and GXE interactions. Courtship success was influenced by a single detected QTL, the main effect of cactus, and 4 GXE interactions, while time to copulation was influenced by 3 different QTLs. Multiple locus REML analysis of courtship song revealed consistent effects linked with the same 4th chromosome markers that influenced time to copulation, a number of GxE interactions, and few possible cases of epistasis. Cuticular hydrocarbon analyses will be discussed.

GxE interactions for fitness and determinants of mate choice can maintain genetic variation in populations, but alter outcomes of sexual selection and isolation, so signal evolution and reproductive isolation may be slowed in diverging populations. Understanding the genetics of adaptation and incipient speciation in D. mojavensis clearly depends on cactus-specific expression of traits associated with host use, courtship behavior, and sexual isolation.

23-07 Poster

IMPROVING CROSS-SPECIES UTILITY OF MICROSATELLITE MARKERS IN SHOREBIRDS AND ALLIES

Clemens Küpper [1], Deborah A. Dawson [2], Tamás Székely [1], Terry Burke [2]

[1] *University of Bath, Department of Biology and Biochemistry, BA2 7AY, Bath, UK*
[2] *University of Sheffield, Department of Animal and Plant Sciences, S10 2TN, Sheffield, UK*

C.Kupper@bath.ac.uk

Charadriiformes (sandpipers, plovers, gulls and auks) have an immense variation in breeding system, migratory strategies and feeding ecology. Many species of this order are endangered and/or declining and thus in need of monitoring and conservation management. However, investigation of population and conservation biology in *Charadriiformes* has been hampered by the lack of appropriate genetic markers, such as microsatellites. Microsatellite markers are highly polymorphic genetic markers frequently used in population and evolutionary genetics. The characterisation of microsatellite markers can take considerable effort and only a few loci can be cross-amplified in other species and then usually only in a narrow taxonomic range (e.g. within the same genus). Here we present a methodology to improve the cross-species utility of microsatellite markers to make them applicable in a broader taxonomic group, so extending their utility across different families within the order *Charadriiformes*. For 55 of 160 *Charadriiformes* microsatellites deposited in the GenBank database we found homologous sequences in the chicken genome with both forward and reverse flanks of the microsatellite repeat in both chicken and the *Charadriiformes* source species conserved. The 55 conserved microsatellites amplified more often than the 10 anonymous microsatellites with 23 conserved microsatellite markers amplifying in a single species from each of the three *Charadriiformes* suborders *Lari*, *Scolopaci* and *Charadri,* whilst none of the anonymous loci did so. Conserved markers were polymorphic in an average of 6.5 out of the 12 *Charadriiformes* species tested suggesting that this method can provide more polymorphic markers to study the molecular ecology of many shorebird species.

23-08 Poster

GENETIC BASIS OF FITNESS DIFFERENCES BETWEEN NATURAL POPULATIONS OF ARABIDOPSIS LYRATA SSP. PETRAEA

Päivi H. Leinonen [1], Annaleena Okuloff [1], Bénédicte Quilot [2], Johanna Leppälä [1], Folmer Bokma [3], Fabian Hoti [4], Mikko Sillanpää [5], Outi Savolainen [6]

[1] *University of Oulu, Department of Biology, PL 3000, 90014, Oulu, Finland*
[2] *French National Institute for Agricultural Research INRA, Plant Breeding and Genetics Department, BP 94, 84143, Avignon, France*
[3] *University of Umeå, Department of Ecology and Environmental Science, 901 87, Umeå, Sweden*
[4] *University of Helsinki, Department of Mathematics and Statistics, PL 3000, 90014, Helsinki, Finland*
[5] *University of Helsinki, Department of Mathematics and Statistics, PL 68, 00014, Helsinki, Finland*
[6] *University of Oulu, Department of Biology, PL 68, 00014, Oulu, Finland*

paivi.h.leinonen@oulu.fi

Local adaptation has been demonstrated in the perennial, outcrossing plant *Arabidopsis lyrata* (Brassicaceae). We have examined the basis of this adaptation by studying differentiation between populations originating from different climatic areas: alpine Norway (Spiterstulen) and continental Germany (Plech). Reciprocal transplant experiments with parental populations have demonstrated population differentiation in several traits. F_2-progeny of crosses between these populations were also grown in both parental population sites. These progeny were used for mapping genomic regions responsible for differences in viability and several life history traits. F_2-plants were genotyped for microsatellites and gene-based markers, many based on candidate genes for flowering time. Recently developed Bayesian mapping methods allowing for an outcross F_2-design and retrospective study of viability were used.

23-09 Poster

LINKAGE MAPPING IN BLUE TITS AND AVIAN COMPARATIVE GENOMICS

Marcus Ljungqvist [1], Bengt Hansson [1]

[1] *Lund University, Animal Ecology, Sölvegatan 37, 223 62, Lund, Sweden*

marcus.ljungqvist@zooekol.lu.se

The Chicken (*Gallus gallus*) genome sequence was recently released and this has triggered research in the evolution of the avian genome. To do comparative genomic studies, one can construct recombination-based linkage maps and then compare gene order and recombination rate in homologous chromosome regions. Such studies have been done recently in Chicken and a passerine bird, the Great reed warbler (*Acrocephalus arundinaceus*). It was found that the gene order was highly conserved between chicken and this passerine bird. On the contrary, the recombination rate was much lower in the warbler than in the Chicken. Also, there was a pronounced difference in recombination rate between the sexes in the warbler, whereas this was not found in the Chicken. To be able to evaluate whether these characteristics are general among passerines, we focused on the Blue tit (*Parus caeruleus*). We have detected many polymorphic markers in this species, and we have scored them in our mapping population to construct a partial linkage map. Interestingly, we found no sex-biased recombination rate in the blue tit, and overall the recombination rate seems to be at an intermediate level between the Chicken and the Great reed warbler, though closer to the Chicken.

23-10 Poster

PATTERNS OF LINKAGE DISEQUILIBRIUM IN A HYBRID PINE, PINUS DENSATA, AND ITS TWO PARENTAL SPECIES

Xiao-Fei Ma [1, 2], Xiao-Ru Wang [1, 2], Pär K. Ingvarsson [2]

[1] *Institute of Botany, Chinese Academy of Sciences, State Key Laboratory of Systematic and Evolutionary Botany, 100093, Beijing, China*
[2] *Umeå University, Umeå Plant Science Centre, Dept. of Ecology and Environmental Science, 90187, Umeå, Sweden*

xiao-ru.wang@emg.umu.se

Linkage disequilibrium (LD) varies among species that have different mating systems. Previous studies show LD decays rapidly in outcrossing species like conifers. Hybrid speciation theory predicts frequent chromosomal rearrangements in the formation of the new species, thus breaking down LD. This has been supported by some studies on artificial hybrids and hybrid zones. However, the patterns of LD are poorly documented in ancient natural hybrids. *Pinus densata* is suggested to have originated from hybridization between *Pinus tabuliformis* and *Pinus yunnanensis*. Populations of *P. densata* have different histories and likely multiple origins. Analysis of LD in the three species could therefore shed light on the genome dynamics associated with hybrid speciation. We sequenced seven genes from 11 natural populations in these three species. No inter-genic LD was found in the three pine species. Average intra-genic LD was low in *P. densata*, in which only 8% of informative sites showing significant associations. LD (r^2) decayed more rapidly in *P. densata* than in the parental species, to less than 0.1 within 200 bp. Adjusted average recombination rate per nucleotide was more than ten times higher in the hybrid than in the parental species, suggesting that chromosome rearrangements and/or recombination occurred frequently in the process of homoploid hybrid speciation as expected from theory. The patterns of LD were markedly different between populations of *P. densata*, demonstrating that patterns of LD are strongly influenced by the evolutionary history of a species.

23-11 Poster

THE GENETIC ARCHITECTURE OF THE PARR-SMOLT TRANSFORMATION IN RAINBOW AND STEELHEAD TROUT (ONCORHYNCHUS MYKISS)

Krista M. Nichols [1], Alicia Felip [2], Paul Wheeler [3], Gary H. Thorgaard [4]

[1] Purdue University, Department of Biological Sciences, 47907, West Lafayette, IN, USA
[2] Instituto de Acuicultura de Torre de la Sal, Consejo Superior de Investigaciones Científicas, 12595, Castellon, Spain
[3] Washington State University, School of Biological Sciences, 99164, Pullman, WA, USA
[4] Washington State University, School of Biological Sciences and Center for Reproductive Biology, 99164, Pullman, WA, USA

kmnichol@purdue.edu

To migrate or to stay is a pervasive theme in the evolution of divergent life history strategies in the animal kingdom. Within the salmonid fishes, variation exists in both the propensity and timing of migration both among and within species. Anadromous salmonids migrate from freshwater to seawater as juveniles, and return to their natal streams to spawn as adults. Prior to migration, a complex physiological transformation culminates in downstream migration, and ultimately enables the fish to adapt to life in the ocean; the genetic basis and evolution of migration, however, is poorly understood. We have begun to dissect the genetic architecture of migration-related physiology and morphology in freshwater resident rainbow trout and migratory steelhead trout (both *Oncorhynchus mykiss*) using quantitative trait loci (QTL) analysis. In doubled haploid progeny produced from a cross between resident and anadromous *O. mykiss*, we have found a single QTL associated with multiple traits including body morphology, skin reflectance and body condition (accounting for 11-28% of the phenotypic variation). This is the only QTL identified when all traits were used in a multiple trait QTL analysis; additional QTL were associated with single traits. Ultimately, this work will contribute to our understanding of the evolution of the continuum of migratory/non-migratory life history types in the salmonid fishes.

23-12 Poster

RECOMBINATION IN ACTION: WHAT LABORATORY AND NATURAL POPULATIONS TELL US

Cinta Pegueroles [1], Héctor Ruiz [1], Marta Pascual [1], Francesc Mestres [1], Joan Balanya [1], Lluis Serra [1]

[1] University of Barcelona, Genetics, Av. Diagonal, 645, 08028, Barcelona, Spain

cpegueroles@ub.edu

The clinal variation of *Drosophila subobscura* chromosomal polymorphism evolves fast and is maintained despite the extensive gene flow detected among populations with microsatellite markers. Traditionally, three selective hypotheses have been advanced to explain the maintenance of the chromosomal polymorphism, according to the level of operation of natural selection: chromosomal, individual genes and coadapted genes (“supergenes”). Deciphering of these mechanisms involves molecular studies of the genic content of chromosomal rearrangements and its recombinational dynamics. Using microsatellite *loci* previously localized by *in situ* hybridization we have obtained a linkage map for the O chromosome for different homokaryotipic lines. High level of recombination has been detected: 90% of individuals presented at least one cross-over and 60% of them more than one recombination event. Recombination rates seem to be fairly uniform along the chromosome although a few mild hotspots of recombination have been observed at a regional scale. The associations between chromosomal inversions in the O chromosome and microsatellite alleles have been studied in two marginal Palearctic populations. The variability in these populations is lower both in terms of microsatellites and inversions. Nevertheless, moderate linkage disequilibrium is observed between inversions and microsatellite *loci* located near their breakpoints. The combined use of these markers over more populations might help us to understand the evolutionary forces on these adaptive clines.

23-13 Poster

MAMMALIAN POPULATION CYCLES: GENETICS OR NOT?

Kaisa Rikalainen [1], Esa Koskela [1], Tapio Mappes [1]

[1] *University of Jyväskylä, Biological and Environmental Science, P.O. Box 35, FIN-40014, Jyväskylä, Finland*

akritvan@cc.jyu.fi

For generations have scientists been interested in periodic fluctuations of population densities in small mammals, voles and lemmings in particular. Despite passionate research, the mechanisms still remain unresolved and a large amount of controversy exists in hypotheses ranging from predation and food shortage to different behavioral patterns. The Chitty model proposes that the changes in population densities are mediated by natural selection operating on the genetic composition of the population. To look into this hypothesis we aim to survey the phases of density cycles of the bank vole *Myodes glareolus*, a common rodent of Northern Europe with a three-year population cycle. Assessing the two peak and two increase phases of bank vole populations in Central Finland by 30 polymorphic microsatellite markers disinters the genetic component of population density fluctuation. Analysis of the temporal genetic shifts associated with population density cycles and the implications of evolution in natural population dynamics will be discussed.

23-14 Poster

TRANSPOSABLE ELEMENTS IN BOREAL DROSOPHILA VIRILIS GROUP SPECIES STUDIED FROM NATURAL POPULATIONS

Liisa Räisänen [1], Jaana O. Liimatainen [1]

[1] *University of Oulu, Department of Biology, P.O. Box 3000, FIN-90014, Oulu, Finland*

liisa.raisanen@oulu.fi

D. virilis group flies, *D. ezoana*, *D. littoralis* and *D. montana* live symparically in northern Europe. Population sizes of *D. littoralis* and *D. montana* have rapidly declined in Fennoscandia since the early 1990´s, whereas abundance of *D. ezoana* has remained fairly constant. As mobilisation of group of unrelated transposable elements produce a syndrome of aberrant traits known as hybrid dysgenesis in *D. virilis*, possible association between transposable elements and population decline are investigated. DNA samples from natural populations of *D. virilis* group species cover of flies from the 1970´s to the present day.

23-15 Poster

LARGE SCALE GENETIC DIFFERENCES BETWEEN THE SEXES IN THE ANT FORMICA AQUILONIA

Jonna Saapunki [1]

[1] *University of Oulu, Department of Biology, P.O. Box 3000, 90014, Oulu, Finland*

jonna.saapunki@oulu.fi

The ant *Formica aquilonia* has been reported to have significant allele frequency differences between the sexes at a few allozyme marker loci in a single population occupying an area of a few hectares. The aim of my study was to expand the earlier work over the genome and to include larger population samples. Thirty eight out of 83 AFLP markers (45%) and 14 out of 17 microsatellites showed significant genetic differences between newly produced males and queens within a nest. Differentiation thus extends over a large part of the genome. A population survey also revealed significant differences between the two female castes, queens and workers. All the samples shared the same mitochondrial haplotype but a Bayesian analysis based on the microsatellites indicated two genetically differentiated clusters of nests within the population. Several cases of apparently non-mendelian inheritance have been reported in ants, including parthenogenesis, genetic caste determination and hybridization. The applicability of the hypotheses in the case of *F. aquilonia* can be evaluated, but none of them can readily explain the data.

23-16 Poster

MULTIPLE ORIGINS OF SELF-COMPATIBILITY IN A. THALIANA

Kentaro K. Shimizu [1], Rie Shimizu-Inatsugi [1], Michael D. Purugganan [2]

[1] *University of Zurich, Institute of Plant Biology, Zollikerstrasse 107, 8008, Zurich, Switzerland*
[2] *New York University, Department of Biology, 100 Washington Square East, 10003, New York, USA*

shimizu@botinst.uzh.ch

The genetic basis of parallel origins of the same phenotype is critical to understanding models of phenotypic evolution. The evolution of selfing from outcrossing species has been described as one of the most prevalent parallel evolutionary transitions in flowering plants. We are taking a candidate gene approach using a worldwide collection of model species Arabidopsis thaliana.

Selfing in this species is associated with different S pseudolocus haplotypes, some of which contain large deletions that are evolutionarily derived from a haplotype with an SCR pseudogene. We sequenced 6 regions in S pseudolocus using 30 accessions of A. thaliana. European accessions have haplotype A, and the pseudogene allele of pseudoSCR1 gene showed the lowest nucleotide diversity, which is a molecular signiture of selective sweep. This support Charles Darwin's reproductive assurance model, stating a positive selection on selfing.

Two other divergent haplotypes (B and C) are found primarily in offshore African islands and Asia. Molecular analysis indicates that S pseudolocus haplotype B contains a novel and possibly functional SCR allele, suggesting that self-compatibility in this species has arisen multiple times with different genetic bases. These results suggest that a single trait, self-compatibility, which is fixed in this species, arose multiple times with different genetic bases. This is the first time that a species-specific trait has been shown to be associated with parallel evolution at the molecular level. The fact that parallel evolution is much more prevalent than is apparent from mere consideration of phenotypic states needs to be considered to study ecologically-relevant genes from natural populations.

23-17 Poster

POLYPLOIDIZATION AND ADAPTIVE RADIATION ALONG WATER-USAGE GRADIENT IN THE GENUS CARDAMINE

Rie Shimizu-Inatsugi [1], Hiroshi Kudoh [2], Kentaro K. Shimizu [1]

[1] *University of Zurich, Institute of Plant Biology, Zollikerstrasse 107, 8008, Zurich, Switzerland*
[2] *Kobe Univeristy, Department of Biology, Rokkoudai-machi 1-1, Nada-ku, 657-8051, Kobe-city, Japan*

inatsugi@botinst.uzh.ch

It is known that more than half of plant species have experienced genome duplication (polyploidization) although the significance of genome duplication is still an open question. S. Ohno proposed that gene duplication is a major motive force for evolution. In contrast, G.L. Stebbins supposed that genome duplication retards adaptive evolution. The aim of this study is to demonstrate the effect of polyploidization through analyzing the adaptive radiation of an Arabidopsis relative, genus Cardamine, along water- usage gradient.

Cardamine has more than two hundreds species. The diploid species live in either wet conditions or open habitats and the polyploid species live in intermediate and fluctuating habitats. The phylogenetic analysis of CHS revealed that most polyploid species originated from the fusion of genomes from various combinations of both wet and open habitats.

Consequently, Cardamine could be a good example to investigate the contribution of polyploidy to an adaptive radiation. We speculate that a polyploid species can survive fluctuating habitat by exploiting the suitable gene set from either of its parental species according to the water environment. The close relationship to Arabidopsis should allow the application of its genomic tools to Cardamine for further analysis.

23-18 Poster

QUANTITATIVE GENETICS IN GREAT REED WARBLERS

Maja Tarka [1], Mikael Åkesson [1], Staffan Bensch [1], Bengt Hansson [1], Dennis Hasselquist [1]

[1] *Lund University, Animal Ecology, Sölvegatan 37, 223 62, Lund, Sweden*

Maja.Tarka@zooekol.lu.se

The population of great reed warblers *Acrocephalus arundinaceus* at Lake Kvismaren, Sweden, was founded in 1978 and has been studied in detail every year since 1983. By using a pedigree with nearly all relationships resolved in the population, measurements of different morphological and fitness-related traits, and a statistical model called the ‘Animal model’, we can make powerful estimates of *e.g.* additive variance and heritability of quantitative traits in the species. One interesting trait in great reed warblers is wing length. A previous study showed that wing length is a highly heritable, sexually dimorphic trait and that there seems to be opposing selection pressures acting on it in males and females. We present results from further analyses of this trait in terms of genetic correlation between male and female wing length and response to selection. Our future aims are to search for QTL’s for wing length and other heritable traits using a recently developed linkage map for great reed warblers.

23-19 Poster

DNA BARCODING IN GREEK FRESHWATER FISH: THE CASES OF DOIRANI AND VOLVI LAKES

Alexander Triantafyllidis [1], Dimitra C. Bobori [1], Christina Koliamitra [1]

[1] *Aristotle University of Thessaloniki, School of Biology, 54124, Thessaloniki, Greece*

atriant@bio.auth.gr

Genetic diversity analyses of species constitute important steps in understanding the mechanisms involved in the adaptation and evolution of the animal species. Furthermore, DNA polymorphism analysis has recently proven to be a reliable, DNA-based taxonomic system, since a single gene sequence can serve as a ' barcode ', sufficient to differentiate all, or at least the vast majority of, animal species. The scope of the present research was to initiate and apply DNA barcoding in Greek freshwater fish species aiming to reveal new approaches on their protection and sustainable management as well as unmask look-alikes to prevent falsification. DNA barcoding has already been applied to North American birds, Australian fish and most recently in tropical Lepidoptera. Based on the methodology that was followed in these studies, in the present study DNA barcoding was carried out in a total of 141 individuals, representing 18 fish species from both lakes Doirani and Volvi (Northern Greece). A 655bp region of the mitochondrial cytochrome oxidase subunit I (cox1) was sequenced using universal primers. Average within-species, -family and -order Kimura two parameter (K2P) distances were 0.41%, 14.9% and 15.6% respectively. All species could be differentiated by their cox1 sequence. Barcoded common species from both lakes had lake-specific haplotypes, indicating that location-based discrimination of species is possible. Although DNA barcoding aims to develop species identification systems, some phylogenetic signal was also apparent in our results. After constructing neighbor joining phylogenetic trees, the clades revealed generally corresponded well with expectations. Our study supports previous studies on the conclusion that cox1 sequencing, or 'barcoding', can be used to identify fish species

24

Sexual selection: testing the alternatives 25 years later

Wednesday August 22 *Location*: Ekonomikum 3

Symposium 24: Sexual selection: testing the alternatives 25 years later

ORGANIZERS: Tom Tregenza, University of Exeter, UK
David Hosken, University of Exeter, UK

09.45-10.15	**Russell Lande** (invited) Some history of sexual selection theory for polygamous species
10.15-10.45	**Rauno Alatalo** (invited) Sexual selection and the indirect genetic benefits
10.45-11.05	**Nina Wedell** Selfish genetic elements and sexual selection
11.05-11.35	*Coffee*
11.35-11.55	**Trine Bilde** The genetic architecture of fitness and evolution of mating biases
11.55-12.15	**Wade Hazel** Is fitness equality necessary for the coexistence of conditionally expressed alternative reproductive phenotypes?
12.15-12.35	**Thomas Getty** Altruism and spite in sexually selected signalling
12.35-14.00	*Lunch, council*
14.00-14.30	**Michael Wade** (invited) The paradox of sexual selection
14.30-14.50	**Jane Reid** Secondary sexual ornamentation and non-additive genetic benefits of female mate choice
14.50-15.10	**Rhonda Snook** Experimental evolution of sexual selection: responses and consequences
15.10-15.30	**Daphne Fairbairn** Sexual selection and allometry: Process does not predict pattern in a water strider
15.30-16.00	*Coffee*
16.00-16.20	**Steve Chenoweth** Dissecting geographical divergence in multiple sexually-selected characters
16.20-16.40	**Roger Härdling** Sexual conflict, genetic correlation and stable polymorphism
16.40-17.00	**Göran Arnqvist** The effect of sexual selection on population fitness
17.00-17.20	**Judith Mank** Evolution of sex-biased genes in birds

24-01 Talk

SOME HISTORY OF SEXUAL SELECTION THEORY FOR POLYGAMOUS SPECIES

Russell Lande [1]

[1] *Imperial College London, Centre for Population Biology, SL5 7PY, Ascot, Berkshire, UK*

r.lande@imperial.ac.uk

Ideas and models of sexual selection in polygamous species will be reviewed, particularly concerning the evolution of mating preferences and sexual dimorphism.

24-02 Talk

SEXUAL SELECTION AND THE INDIRECT GENETIC BENEFITS

Rauno V. Alatalo [1]

[1] *University of Jyväskylä, Department of Biological and Environmental Sciences, PO Box 35, FI-40014, Finland*

alatalo@bytl.jyu.fi

Sexual selection is a strong evolutionary force as already recognized by Darwin. However, in spite of the great interest in the study of sexual selection over the past decades, it remains unclear how important the indirect genetic benefits are for the evolution of mate choice. Indeed, the notion of the lek paradox, emphasizing that genetic benefits in terms of the enhanced offspring fitness cannot be large enough to allow mate choice, remains as a major question. Obviously, sexual selection through intrasexual competition or through intersexual selection for any direct benefits may have much stronger effects on the fitness of the choosy sex. Also, in many mating systems mate choice is heavily restricted by the male-male combat. Thus, any indirect genetic benefits frequently cannot be driving mate choice, even if there might be genetic consequences for the offspring fitness. However, there are many mating systems, where costs of mate choice are practically negligible, which may allow mate choice for the indirect benefits that affect only the offspring fitness. The main problem in the research is the very weak correlations that the indirect benefits might exhibit. The weak effect sizes imply that selective publishing continues to be a major threat in the current research. Thus, we need comprehensive studies dealing with the costs of mate choice, mate preferences in relation to sexual traits, and of the genetic and environmental determinants of the sexual traits to reveal the true possibility for indirect benefits.

24-03 Talk

SELFISH GENETIC ELEMENTS AND SEXUAL SELECTION

Nina Wedell [1], Thomas A. R. Price [1], Greg D. D. Hurst [2]

[1] *University of Exeter, School of Biosciences, Cornwall Campus, TR10 9EZ, Penryn, UK*
[2] *University College London, Department of Biology, 4 Stephenson Way, NW1 2HE, London, UK*

N.Wedell@Exeter.ac.uk

Conflicts between genetic components within an organism involving both nuclear and cytoplasmic genes are common. Selfish Genetic Elements (SGEs) are genes, organelles or microorganims present within the genome or cell of an organism that employ various tactics to increase their transmission rate relative to the rest of the genome to the next generation. SGEs occur in all living organisms, often making up a large part of the genome and can reach high prevalence promoting opposing selection to halt their spread. SGEs are important agents in the evolution of genetic architecture and sex determination systems, but little attention has been paid to the role SGEs may play in sexual selection. Here we discuss the impact of a SGE - X-linked meiotic drive (SR) – on reproductive behaviour in the fly Drosophila pseudoobscura. SR drive results in female only broods due to elimination of Y-bearing sperm during meiosis. However, SR males are poor sperm competitors, ensuring polyandrous females sire a higher proportion of males and thereby providing females with a 'behavioural' mechanism to increase their fitness. We present results showing that polyandry is favoured in the presence of SR. In addition, promiscuity may reduce population extinction risk and the presence of SR promotes the evolution of increased female remating rate. These results demonstrate the potency of SGEs in affecting sexual selection.

24-04 Talk

THE GENETIC ARCHITECTURE OF FITNESS AND EVOLUTION OF MATING BIASES

Trine Bilde [1]

[1] *Uppsala University, Evolutionary Biology Centre, Norbyvägen 18d, 752 36, Uppsala, Sweden*

trine.bilde@biology.au.dk

The evolution of mate choice by indirect selection rests on the assumption that mate choice is directed towards genetically superior individuals. The choosy sex, usually females, achieves indirect benefits by mating with mates of high genetic quality because their offspring inherit the underlying genes for quality and the associated mating preference. These indirect benefits can arise either from specific superior male genotypes (good genes), or from male genotypes that result in superior offspring fitness in combination with specific female genotypes – (compatible genes). A "good gene" is an allele that increases fitness independent of the architecture of the remaining genome and show additive genetic variation. A "compatible gene" is defined as an allele that increases fitness when it is paired with a specific homologue (dominance) or allele at another gene locus (epistasis), and compatible genes show nonadditive genetic variation across the genome. The objective of this study was to partition genetic variation of fitness traits into additive and nonadditive components. For this purpose we performed a full diallel reciprocal cross using 19 inbred female lines ($F=0.89$) of the bean weevil *Callosobruchus maculatus*. This quantitative genetic design partitions phenotypic variance into six additive and nonadditive genetic variance components. We measured fecundity, egg hatching rate, total offspring and total grand-offspring production and found relatively low additive genetic variation for these traits, and significant non-additive genetic variation for some components including sex-specific effects. These findings are discussed in relation to indirect selection and the evolution of mating biases.

24-05 Talk

IS FITNESS EQUALITY NECESSARY FOR THE COEXISTENCE OF CONDITIONALLY EXPRESSED ALTERNATIVE REPRODUCTIVE PHENOTYPES?

Wade Hazel [1], Richard Smock [2], Joseph Tomkins [3]

[1] *DePauw University, Biology, 46135, Greencastle, Indiana, USA*
[2] *DePauw University, Mathematics, 46135, Greencastle, Indiana, USA*
[3] *University of Western Australia, Centre for Evolutionary Biology, 6009, Crawley, Western Australia, Australia*

wnh@depauw.edu

Alternative reproductive phenotypes are hypothesized to be common outcome of sexual selection. The alternatives can represent the canalized expression of genetic differences (alternative strategies), or plastic/conditional responses (a conditional strategy). Population genetic theory indicates that for alternative strategies to coexist, their average fitness must be equal. However, in the case of conditionally expressed alternative phenotypes, there is disagreement over whether equality of average fitness of the alternatives is necessary. We briefly review the arguments having to do with the fitness of conditionally expressed alternative phenotypes. We then propose a quantitative genetic approach to the production of alternative phenotypes that resolves the disagreement. The model treats alternative phenotypes as products of an environmentally-cued threshold trait, where both heritable variation in response to some cue and variation in the strength of the cue determine the frequencies of the alternative phenotypes. The model shows that if cues are statistically related to the fitnesses of the alternative phenotypes, such that the fitness functions of the alternative phenotypes intersect at some value of the cue, then the response to the cue will evolve to a stable equilibrium value. In contrast to current views that hold considerable currency, this value is not necessarily equivalent to the intersection of the fitness functions of the alternative phenotypes, and the alternative phenotypes can coexist in the population at equilibrium regardless of whether their average fitness is equal or unequal.

24-06 Talk

ALTRUISM AND SPITE IN SEXUALLY SELECTED SIGNALING

Thomas Getty [1]

[1] *Michigan State University, Department of Zoology & Kellogg Biological Station, 3700 E. Gull Lake Dr., Hickory Corners, MI 49060, USA*

getty@msu.edu

Sexual selection for reproductive advantage has driven the rapid evolution of a great diversity of spectacular displays and subtle preferences. Theoretical models of signaling games have difficulty explaining this. When signalers act selfishly, there is a high barrier to the initiation of signal-preference co-evolution. Sexual selection results from social interactions. W.D. Hamilton revolutionized our understanding of social dynamics when he formalized the concepts of kin selection and inclusive fitness. Here I develop an inclusive fitness approach to inter-sexual selection and show that altruism can lower the barrier to the initiation of sexual selection and spite can drive signal-preference co-evolution to greater extremes. Spite is usually expected only in small groups of competitors with some form of kin discrimination. It is effective here, even in large groups without male kin recognition, because discriminating females selectively reject males with small displays. Females and high quality males have a mutual interest in females being able to discriminate and reject low quality males, who are vulnerable because they pay disproportionately high costs to stay in the signaling game. The inclusive fitness approach opens up a dramatic new perspective on sexual selection. There is increasing evidence that sexual selection plays a role in speciation. This suggests that altruism and spite could be important dynamics in the evolution of biodiversity.

24-07 Talk

THE PARADOX OF SEXUAL SELECTION

Michael J. Wade [1]

[1] *Indiana University, Department of Biology, 1001 East 3rd Street, Bloomington, IN 47405, USA*

mjwade@indiana.edu

The macro-evolutionary pattern of large phenotypic differences between males of related species is the signature of a very strong evolutionary force. However, selection acting on only one sex is slower and weaker by half than selection acting on both sexes. Selection acting in opposing directions, such as for an exaggerated trait in males but against the same trait in females, is even slower and weaker. Selection is further weakened by trade-offs between fitness components, such as enhanced reproductive fitness that comes at the expense of viability fitness. This the Paradox of Sexual Selection: How do exaggerated male traits evolve and differentiate so rapidly if the strength of selection on them is so weak? The Opportunity for Selection allows us to measure the sex-difference in the strength of selection (the variance in relative fitness) and understand why selection acting on males can be much stronger than that acting on females. Molecular methods for determining maternity and paternity of offspring in populations and recent developments in molecular evolutionary theory allow us to characterize the strength of sexual selection and detect the genomic signature of sexual selection.

24-08 Talk

SECONDARY SEXUAL ORNAMENTATION AND NON-ADDITIVE GENETIC BENEFITS OF FEMALE MATE CHOICE

Jane M. Reid [1]

[1] *University of Aberdeen, School of Biological Sciences, Zoology Building, Tillydrone Avenue, AB24 2TZ, Aberdeen, Scotland*

jane.reid@abdn.ac.uk

Ornamental secondary sexual traits are hypothesised to evolve in response to directional mating preferences for more ornamented mates. Such mating preferences may themselves evolve partly because ornamentation indicates an individual's additive genetic quality ('good genes'). While mate choice can also confer non-additive genetic benefits ('compatible genes'), the identity of the most 'compatible' mate is assumed to depend on the choosy individual's own genotype. It is therefore unclear how choice for non-additive genetic benefits could contribute to directional mating preferences and consequently the evolution of ornamentation.

I show that in free-living song sparrows (*Melospiza melodia*), individual males varied in their kinship with the female population. Furthermore, a male's song repertoire size, a secondary sexual trait, was negatively correlated with kinship such that males with larger repertoires were less closely related to the female population. After excluding close relatives as potential mates, individual females were on average less closely related to males with larger repertoires. Therefore, female song sparrows expressing directional preferences for males with larger repertoires would on average acquire relatively unrelated mates and produce relatively outbred offspring. I discuss the mechanisms underlying the observed correlations between ornamentation and relatedness and their likely generality, and suggest that such non-additive genetic fitness benefits of directional mating preferences should be incorporated into genetic models of mate choice and sexual selection.

24-09 Talk

EXPERIMENTAL EVOLUTION OF SEXUAL SELECTION: RESPONSES AND CONSEQUENCES

Helen S. Crudgington [1], Steve J. Martin [1], Lucy Friend [1], Rhonda R. Snook [1]

[1] *University of Sheffield, Department of Animal and Plant Sciences, S10 2TN*

r.snook@sheffield.ac.uk

Twenty-five years ago, sexual selection was poised to dominate much of the coming evolutionary and behavioural research. One discussion then was the role of comparative and experimental work in examining how sexual selection influenced the evolutionary trajectories within and between populations. Over the past decade, experimental evolution has been embraced as one strategy to elucidate how sexual selection operates on populations. Here we report recent findings on the action of sexual selection in the promiscuous fruit fly, *Drosophila pseudoobscura*, where we have experimentally either enforced monogamy or elevated promiscuity. We discuss several male traits, including behavioural, physiological and morphological characters, which have changed as a consequence of the manipulation of sexual selection and demonstrate female preference for some of these traits. We also describe the action of sexual conflict in these experimental lines, a topic that was discussed as an alternative 25 years ago and which has seen recent rampant expansion.

24-10 Talk

SEXUAL SELECTION AND ALLOMETRY: PROCESS DOES NOT PREDICT PATTERN IN A WATER STRIDER.

Daphne J. Fairbairn [1], Angeline Bertin [2]

[1] *University of California at Riverside, Department of Biology, 900 University Avenue, 92521, Riverside, California, USA*
[2] *Southwest Foundation for Biomedical Research, Department of Genetics, 900 University Avenue, 92521, San Antonio, Texas, USA*

daphne.fairbairn@ucr.edu

Male genital morphology in insects and arachnids is characterized by static hypoallometry and low intrapopulational levels of phenotypic variation relative to other male traits. We use data from field and laboratory populations of the water strider, *Aquarius remigis*, to test the hypothesis that this pattern reflects stabilizing sexual selection on genital traits, a hypothesis known as the "one-size-fits-all model of genital evolution". We test this by comparing the patterns of selection, allometry and trait variation for a set of genitalic and somatic morphological traits. We show that the patterns of variation and scaling of these traits differ sharply from those predicted by the one-size-fits-all hypothesis. Specifically, the male genital structures show static hypoallometry and low intrapopulational levels of phenotypic variation, in spite of consistent, strong, directional sexual selection. Our data clearly refute the assumption that hypoallometric scaling of genitalic traits implies stabilizing selection. We discuss the implications of this finding with respect to sexual selection and genitalic evolution in arthropods, and more generally, with respect to functional interpretations of allometric trends within and among populations.

24-11 Talk

DISSECTING GEOGRAPHICAL DIVERGENCE IN MULTIPLE SEXUALLY-SELECTED CHARACTERS

Steve F. Chenoweth [1], Howard D. Rundle [2], Mark W. Blows [1]

[1] *University of Queensland, School of Integrative Biology, St Lucia, 4072, Brisbane, Australia*
[2] *University of Ottawa, Department of Biology, K1N 6N5, Ottawa, Canada*

s.chenoweth@uq.edu.au

Identifying the processes by which natural populations have diverged in phenotype is a major goal of evolutionary genetics. For traits known to experience sexual selection, there are remarkably few empirical data that can shed light on the relative contribution of sexual selection to trait divergence as compared with drift and natural selection. Here, using two large experiments in the fruit fly *Drosophila serrata*, consisting of both estimates of phenotypic sexual selection, and additive genetic variance and covariance within and among natural populations, we dissect patterns of multitrait divergence in eight sexually-selected display traits among nine natural populations. We show how these approaches can be used to identify genetically independent aspects of differentiation among natural populations, which can be associated with different putative selective agents and identify how natural populations have diverged along major or minor lines of genetic variance.

24-12 Talk

SEXUAL CONFLICT, GENETIC CORRELATION AND STABLE POLYMORPHISM

Roger Härdling [1]

[1] *Lund University, Animal Ecology, Ecology Building, 223 62, Lund, Sweden*

roger.hardling@zooekol.lu.se

Evolutionary conflict between the sexes is predicted to lead to sexual arms races. Male adaptations for acquiring matings ("offence" traits) spread in spite of a harmful effect on female partners, and are met by female counteradaptations that increase female fitness e.g. by reducing mating rate. Like any evolutionary process, the dynamics of sexual antagonistic coevolution is influenced by direct as well as indirect selection forces. I will present theoretical result showing that antagonistic coevolution may lead to a stable state where multiple pairs of male and female conflict adaptations are maintained in the same population (i.e. stable polymorphism), due to a negative feedback from male evolution on female fitness. Genetic correlation between the sexes strengthens the stability of the equilibrium under sexual conflict, unlike when female choice dictates the course of evolution. In addition, polymorphic populations are less easy to invade for new conflict adaptations, which may have consequences for the dynamics of the antagonistic coevolution. I will discuss the results in the context of gene-flow between allopatric populations, and argue that the process may be a general force that maintains variation within populations.

24-13 Talk

THE EFFECT OF SEXUAL SELECTION ON POPULATION FITNESS

Göran Arnqvist [1], Claudia Fricke [1]

[1] *Uppsala University, Ecology and Evolution, Norbyv 18D, SE75236, Uppsala, Sweden*

Goran.Arnqvist@ebc.uu.se

The role of sexual selection in adaptation is controversial and different models of sexual selection male distinct predictions. Some models suggest that the rate of fixation of beneficial alleles increases or that deleterious alleles are purged more effectively under sexual selection. Other models suggest that sexual selection can instead impose a load on populations and cause non-adaptive evolution even to the point of extinction. Thus, sexual selection can both accelerate and impede the rate of adaptation to novel environments. There is, however, little consensus with regards to whether natural and sexual selection generally reinforce one another or, conversely, act in opposite directions in adaptive evolution. I will briefly review this topic and will discuss an artificial selection experiment, using the seed beetle *Callosobruchus maculatus*, where we experimentally removed sexual selection in half of our replicate lines. We found that sexual selection accelerated adaptation under directional natural selection while sexual selection depressed population fitness under stabilizing natural selection. Such interactions between natural and sexual selection will complicate tests of sexual selection theory based on assessments of the effects of sexual selection on population fitness.

24-14 Talk

EVOLUTION OF SEX-BIASED GENES IN BIRDS

Judith E. Mank [1]

[1] *Uppsala University, Department of Evolutionary Biology, Sweden*

judith.mank@ebc.uu.se

The powerful selective pressures of mating and sperm competition are thought to result in a faster rate of evolution in sex-biased genes, with male-biased genes experiencing the fastest rate of functional change. This effect has been documented for genes directly involved in reproduction, but little is known about the rate of evolution sex-biased genes in somatic tissue, which often form the basis of intra-sexual competition and mate choice. We used microarray data to identify genes that are expressed more in one sex relative to the other in the brains of chicken embryos, as these genes likely form the basis of neurological and behavioral differences between the sexes that function in pre-mating sexual selection. We then compared the rate of evolution, or the ratio of non-synonymous (coding) to synonymous (silent) mutations (d_N/d_S), for sex-biased versus unbiased brain genes in a dataset of 4127 coding regions aligned between chicken and zebra finch, which corresponds to roughly a quarter of all known avian genes. While sex-biased genes showed a significantly higher d_N/d_S ratio than unbiased genes, the effect was almost entirely due to female-biased genes. If not a function of non-adaptive mechanisms having to do with male-biased gene expression, this may be explained by the importance of mate recognition and female choice in avian reproduction.

24-01 Poster

EXTRAPAIR FERTILIZATIONS AND THE OPPORTUNITY FOR SEXUAL SELECTION IN LONG-DISTANT MIGRATORY PASSERINES

Tomas Albrecht [1], Jakub Kreisinger [1]

[1] *Charles Univ Prague, Zoology, Vinicna 7, CZ12844, Prague, Czech Republic*

albrecht@ivb.cz

Extrapair fertilizations (EPFs) are frequently documented in songbirds; however, the reason why this reproductive tactic contributes to variance in male reproductive success and hence the strength of sexual selection more in some species than others remains little studied. Here we use comparative approach to test the hypothesis that migration and/or breeding synchrony could promote the contribution of EPFs to variance in male fitness in north temperate songbirds. Comparative data reveal that the opportunity for sexual selection due to EPFs is positively associated with both migration distance and breeding synchrony when statistically controlled for the length of breeding season and proportion of extrapair young with assigned genetic sires. In general, these data suggest that EPFs have a potential to play an important role in the evolution of sexually selected traits in long-distance migratory songbirds of Europe and North America. We discuss several mechanisms that could extend these relationships.

24-02 Poster

SEXUAL SELECTION AND THE EVOLUTION OF FEMALE REPRODUCTIVE TRACT MORPHOLOGY

Leonardo D. Bacigalupe [1], Allen J. Moore [2], Rhonda R. Snook [3]

[1] *University of Sheffield, Department of Animal & Plant Sciences, S10 2 TN, Sheffield, UK*
[2] *University of Exeter, Centre for Ecology and Conservation, School of Biosciences, S10 2 TN, Penryn, UK*
[3] *University of Sheffield, Department of Animal & Plant Sciences, TR10 9EZ, Sheffield, UK*

L.Bacigalupe@sheffield.ac.uk

Sexual selection acts upon traits that affect the mating success of both sexes. When females are promiscuous, sexual selection also acts after copulation and can comprise both sperm competition and cryptic female choice. In internally fertilizing species, these evolutionary forces come into play in the female reproductive tract (FRT). Comparative and experimental evidence suggest that FRT morphology may be a potent force of postcopulatory sexual selection. Our aim was to explore the role of the risk of sperm competition as a potential driver of FRT morphology. In particular, we tested whether the risk of sperm competition (RSC) affected the evolutionary trajectories of FRT morphology. We used a set of experimentally evolved populations of the promiscuous *Drosophila pseudoobscura*, in which the RSC was manipulated by either increasing or decreasing the natural levels of female promiscuity. We determined spermathecal area, the length of its corresponding duct and the length of the distal and proximal parts of the seminal receptacle in full-sibs and half-sibs daughters from a breeding design applied to each of the three selection treatments. Our results showed that, in lines with a higher RSC, FRT morphology is more tightly integrated than in lines that have evolved with lower or no RSC. While these differences were not translated into statistical differences among the three **G**-matrices, it seems that RSC can drive the evolutionary trajectory of FRT morphology.

24-03 Poster

GENETIC ARCHITECTURE OF SEXUAL SELECTION IN THE GUPPY.

Geir H. Bolstad [1], Line K. Larsen [1], Christophe Pélabon [1], Gunilla Rosenqvist [1]

[1] *Norwegian university of science and technology, Department of Biology, Høgskoleringen 5, Realfagbygget, 7491, Trondheim, Norway*

geir.bolstad@bio.ntnu.no

Evolution of male ornaments via female preference requires genetic correlation between the female choice and the male ornament. Genetic correlation can be caused either by pleiotropy, physical linkage, or linkage disequilibrium. In absence of selection, genetic correlations between two traits due to linkage disequilibrium are expected to rapidly disappear due to recombination. To test whether the genetic correlation between female preference and male ornament observed in Guppy is due to pleiotropy / strong physical linkage or linkage disequilibrium, we compared the correlation between these traits among 40 captive populations maintained for nine generations with or without sexual selection. If the correlation is due to linkage disequilibrium, it should be broken in the populations where sexual selection was absent. Knowledge of the mechanism underlying the correlation between traits is fundamental in understanding the constraints of evolution on these traits, and may have implications for breeding programs where control of the mating often prevents sexual selection.

24-04 Poster

SEXUALLY SELECTED ORNAMENTS AND THE POTENTIAL FOR SELECTION, A CASE STUDY

Elisabeth Bolund [1], Holger Schielzeth [1], Wolfgang Forstmeier [1]

[1] *Max Planck Institute for Ornithology, Behavioural Ecology & Evolutionary Genetics, Postfach 1564, 82305, Starnberg (Seewiesen), Germany*

bolund@orn.mpg.de

Sexually selected ornaments are well studied in many species and recently, the study of the potential for selection of sexually selected traits in extant populations has gained momentum. Thus, the question to answer is, to what extent selection is acting on the genetic component of a sexually selected trait, so that change can accumulate over generations, and conversely, to what extent selection is acting on the environmental component of the trait, thus leading to no change over generations. By dividing the phenotypic variance of a trait into its breeding value, which is an estimate of the genetic component, and the environmental deviation from the breeding value, it is possible to address this question and ascertain to what extent there is potential for the trait to change over generations.

We approach this issue using a captive population of zebra finches, a common model organism in the study of sexual selection. We measured a range of sexually selected traits in 500 male zebra finches, namely: beak colour, song rate, song structure, and body size (tarsus length and body mass). A subset of the population was allowed to breed under semi-natural conditions in aviaries. To address the question of potential for selection, we used the animal model to obtain estimates of the breeding value and the environmental deviation from the breeding value of the sexually selected traits. I will present results relating the reproductive performance of males to their phenotype, their breeding value and the environmental deviation from the breeding value, thereby addressing the issue of the potential for selection on sexually selected traits in this model organism.

24-05 Poster

PANORPA ALPINA: MULTIVARIATE ANALYSIS OF LIFE HISTORY

Gerhild Bornemann [1], Klaus Peter Sauer [1]

[1] *Rheinische Friedrich-Wilhelms-Universität Bonn, Institute of Evolutionary Biology and Ecology, An der Immenburg 1, 53121, Bonn, Germany*

gbornemann@evolution.uni-bonn.de

Condition-dependent mating behaviour is a characteristic property of scorpionfly mating systems. We present a description of the mating system of *P. alpina* (Mecoptera: Panorpidae) on the basis of data collected during lifetime observations of enclosure populations. The main focus of interest was the delivery of nuptial gifts as a condition-dependent component of male behaviour. In addition to analysis with common statistical methods we carried out a multivariate analysis using a pathmodel to investigate the influence of condition on various life history traits and its relation to reproductive success.

24-06 Poster

EVOLUTIONARY POTENTIAL OF SEXUAL SIZE AND SHAPE DIMORPHISM IN A BLOODSUCKING INSECT

Carezza Botto-Mahan [1], Carmen Gloria Ossa [1], Rodrigo Medel [1]

[1] *Universidad de Chile, Facultad de Ciencias, Departamento de Ciencias Ecologicas, Santiago, Chile*

cbotto@uchile.cl

Sexual selection is one of the main mechanisms to explain sexual size dimorphism (SSD). In species where males are larger than females, intrasexual selection by male competition could explain this difference. However, in the reverse situation, where females are larger than males, natural selection acting on the correlation between size and fecundity, may account for this phenomenon, especially if female reproductive success is resource limited. In spite of the importance of assessing selection on female and male components, few studies have quantified selection acting in the two sexes simultaneously. Quantitative genetic theory predicts that SSD evolution is a slow process if the genetic correlation for size between sexes is close to the unit, and if size heredability is similar in both genders. In this study we examine the evolutionary potential in the sexual size and shape dimorphism of a triatomine hemipteran, Mepraia spinolai, by using geometric morphometrics and a quantitative genetic model. Males and females of this species show SSD at adulthood. Females are larger than males in body length and legs, and their abdomens are wider. We examine the relationship between abdomen width and female reproductive investment, and size and shape heredability in a half-sib design using 40 sires and 120 full-sib maternal families. Results indicate that investment in reproductive tissue correlates significantly with body size and with the amount of ingested blood along their ontogeny. This result implies that female reproductive potential is resouce limited, which verifies one of the elements to explain SSD. Size and shape heredability, in turn, was consistently higher in males than females indicating that males have a higher evolutionary potential than females. Overall, our results suggest that even though selection on females is the most important mechanisms underlying SSD in M. spinolai, males have an important genetic variation to track female size evolution. FONDECYT 3050033.

24-07 Poster

THE EFFECT OF SOCIAL ENVIRONMENT ON THE EVOLUTION OF SPERM EJACULATES IN THE COCKROACH NAUPHOETA CINEREA

Casper J. Breuker [1], Martin Edvardsson [1], Patricia J. Moore [1], Allen J. Moore [1], John Hunt [1]

[1] *University of Exeter, Cornwall Campus, Centre for Ecology and Conservation, TR10 9EZ, Penryn, Cornwall, United Kingdom*

casper_j_breuker@yahoo.co.uk

A diversity of animals species are known to adjust their ejaculate characteristics in response to the risk of sperm competition. Very little, however, is known about the underlying genetics of this plasticity. In the cockroach, *Nauphoeta cinerea*, dominant males do get more mating opportunities than subordinate males. Consequently, the risk of sperm competition varies with dominance status in this species. Here we examine the underlying genetics of ejaculate characteristics (spermatophylax and ampulla size, sperm number and morphology) in *N. cinerea* in a half-sib genotype-by-environment breeding design where we experimentally manipulated the social environment of the genetic male using pheromones added to an unrelated, random male. In this talk, we will present the results of this experiment and discuss the importance of the social environment to the evolution of male ejaculate characteristics

24-08 Poster

EFFECTS OF DIVERSITY AND RELATEDNESS ON OFFSPRING SURVIVAL

Sofia Caesar [1], Anders Forsman [1], Magnus Karlsson [1]

[1] *University of Kalmar, School of Pure and Applied Natural Sciences, 391 82, Kalmar, Sweden*

sofia.caesar@hik.se

Heterogeneous offspring may confer advantages to females that inhabit variable environments. Producing a diverse set of progeny may reduce the probability that all offspring become ill-suited to future conditions. Increased phenotypic diversity may also reduce competition among siblings. Females of the colour polymorphic pygmy grasshopper, *Tetrix subulata,* mate polyandrously and offspring diversification, with regard to color morph, increases with the number of putative sires. Color morphs represent alternative strategies that differ in body size, physiology, behavior and life-history. Here, we experimentally evaluate the roles of relatedness and among-sibling diversity for offspring survival. We created "family-groups" that consisted of newly hatched offspring from one, three or seven different mothers. We manipulated the degree of competition by rearing the nymphs under either high or low density (six or fifteen individuals per bucket). We find that survival was negatively influenced by crowding, suggesting that competition is important. Survival increased with increasing colour morph diversity, suggesting that competition is weaker among individuals that belong to different colour morphs and utilize slightly different resources. Survival was also enhanced by relatedness, suggesting that non-sibling individuals compete more strongly for resources. These findings point to an important benefit of producing diverse offspring.

24-09 Poster

DO FEMALES EXPERIENCE COSTS FROM MATING WITH HIGHLY ORNAMENTED MALES?

Patricia Celis [1], Jefferson A. Graves [2], Diego Gil [3]

[1] St. Andrews University, Biology, School of Biology, HMB. St. Andrews University, KY169TH, St. Andrews, Fife, U.K.
[2] St. Andrews University, Biology, School of Biology, HMB. St. Andrews University, KY169TH, St. Andrews, U.K.
[3] Museo Nacional de Ciencias Naturales, Ecologia Evolutiva, MNCN, Jose Gutierrez Abascal 2, E-28006, Madrid, Spain

pc31@st-andrews.ac.uk

The acceptance of polygyny by females has long posed a problem for evolutionary biologists. The polygyny threshold model (Orians 1969) provided a solution, proposing that females could benefit from mating polygynously if the benefits were greater than the costs. However, this model did not address the costs for primary females. Several tests of this model have been conducted, but these are not conclusive and lack a complete analysis of possible costs. For instance, little attention has been paid to additional ways by which females might increase their fitness, such as nest parasitism of the primary female or biased sex-ratios.

Here, we assess the costs experienced by spotless starling females mated to males that varied in a plumage ornament (length of their throat feathers), a character considered positively associated with the degree of polygyny. We followed 69 nest-boxes during two reproductive seasons and measured the number, sex and quality of fledglings. Mates of monogamous and primary females were identified during feeding observations. We also performed a manipulation of the throat feather length. We found a negative correlation between the length of the throat feathers and two measures of reproductive success: chick weight and number of fledglings. Males with shortened throat feathers provided more paternal care to their broods, which in turn produced significantly more fledglings and had more female-biased sex-ratios than control broods. These results support the theory that primary females can experience direct costs from mating with polygynous males through a differential allocation of male parental effort. We propose that adjusting the offspring sex-ratio could be used by females to compensate for these costs.

24-10 Poster

ADAPTIVE PLASTICITY IN FEMALE CHOICE OF MALE SEXUALLY SELECTED ORNAMENTS

Alexis S. Chaine [1, 2], Bruce E. Lyon [2]

[1] Station d'Ecologie Experimentale du CNRS, Evolution et Diversite Biologique, Station du CNRS a Moulis, 09800, Moulis, France
[2] University of California, Santa Cruz, Ecology and Evolutionary Biology, EMS Bldg, 95064, Santa Cruz, CA, USA

alexis.chaine@lsm.cnrs.fr

Models of the evolution of male sexual ornaments via female choice assume consistent directional mate preferences, yet this assumption is rarely tested and could greatly alter our perspective on the evolution of sexual characters. We studied female preferences for male color ornaments and body size in a wild population of the lark bunting, *Calamospiza melanocorys*, across five years. Female preferences were highly variable across time - no two years were alike - with some traits showing changes in the direction of the preference in different years. By tracking preferences of females present in multiple years, we show that this shift in average population preference is the result of plasticity in mate choice of individual females rather than other processes. This result indicates much more complexity in female choice decisions than have been previously assumed. Examination of some causes for flexible female choice reveal that fluctuations in female decisions are in part associated with direct benefits related to raising offspring which likely change from year to year. Because such preferences may depend on the social and ecological context of choice, results from choice trials in controlled settings may mask complexity of female behaviors. By looking at such patterns across years, we gain a much richer understanding of selection dynamics on sexual ornaments and find evidence for new mechanism for the evolution of multiple ornaments: males who present multiple signals a more likely to be chosen by females under different social and ecological contexts.

24-11 Poster

EXTRAORDINARY FLUX IN SEX-RATIO

Sylvain Charlat [1, 2], Emily A. Hornett [1], James H. Fullard [3], Neil Davies [2], George K. Roderick [4], Nina Wedell [5], Gregory D. D. Hurst [1]

[1] *University College London, Department of Biology, 4 Stephenson Way, London NW1 2HE, UK*
[2] *University of California Berkeley, Gump South Pacific Research Station, BP 244 Maharepa, 98728 Moorea, French Polynesia*
[3] *University of Toronto at Mississauga, Department of Biology, 3359 Mississauga Rd, N., Mississauga, Ontario Canada L5L 1C6*
[4] *University of California, Environmental Science (ESPM), Berkeley, California 94720-3114, USA*
[5] *University of Exeter, School of Biosciences, Cornwall Campus, Tremough, Penryn TR10 9EZ, UK*

s.charlat@ucl.ac.uk

The ratio of males to females in a species is often considered to be relatively constant, at least over ecological time. Forty years ago, Hamilton noted that the spread of ‘selfish’ sex-ratio distorting elements could be rapid and produce a switch to highly biased population sex-ratios (Hamilton 1967). The move to a highly skewed sex-ratio is known to engender the spread of mutations that suppress the sex-ratio distortion. We present evidence from the butterfly *Hypolimnas bolina* that the suppression phase can be extremely fast, with a switch from a 100:1 population sex-ratio to 1:1 occurring in fewer than 10 generations.

References

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24-12 Poster

ECOLOGICAL CAUSATION OF INTERSEXUAL MIMICRY IN HAWAIIAN DAMSELFLIES

Idelle A. Cooper [1]

[1] *Indiana University - Bloomington, Evolution, Jordan Hall, 1001 E. 3rd St., 47405, Bloomington, IN, USA*

idcooper@indiana.edu

The cause of phenotypic differences between sexes has long attracted the attention of biologists. While sexual dimorphism is almost exclusively attributed to sexual selection, the role of natural selection remains poorly understood. My research indicates that natural selection plays a major role in the evolution of female and male color types in the Hawaiian damselfly, *Megalagrion calliphya*. Although most species in this genus exhibit sexual dimorphism in color (red males and green females) this species contains a female-limited dimorphism in which the male color is expressed by some females. Such female-limited dimorphisms are common in odonates, but the adaptive significance remains unknown. Previous studies examined whether male mimicry allows females to avoid costly sexual interactions but found no evidence for sexual selection. Here, I examine the ecological distribution and selection pressures on the two morphs to understand the role of natural selection in determining this trait. The male-colored females increase in frequency from 0% to 97% over an elevational increase of 1400 meters. Along that gradient, maximum temperature and solar radiation also increase. Additionally, a field transplant experiment to test the effect of solar radiation on female body temperature suggests that male coloration in females is adaptive for thermal balance in the exposed habitat found at high elevations. This research is novel in suggesting that intersexual mimicry could arise as a consequence of natural selection rather than sexual selection.

24-13 Poster

BRIDGING, A NEGLECTED DISPERSAL MODE THAT CAN EXPLAIN THE EVOLUTION OF EXTREME SSD IN SPIDERS

Guadalupe Corcobado [1], Miguel A. Rodriguez-Girones [1], Eva De Mass [2, 1], Jordi Moya-Laraño [1]

[1] Estación Experimental de Zonas Áridas / CSIC, Departament of Functional Ecology and Evolutionary, C/ General Segura Nº 1, 04001, Almería, Spain
[2] Universitat de Barcelana, Department of Animal Bilogy, Avda.Diagonal Nº 645, 08028, Barcelona, Spain

gmarquez@eeza.csic.es

Numerous hypotheses try to explain the adaptive evolution of SSD in spiders. The Gravity Hypothesis (GH) is the first hypothesis that provides a powerful explanation for when extreme SSD is to be expected. According to the GH, extreme SSD evolves in spiders that live in tall places because smaller males have a mating advantage during scramble competition by climbing faster. However, besides climbing, males have to bridge to reach females. To bridge, a spider releases a line of silk into the air that will attach to a distant plant, and then walks to the end point hanging from this line. To test if bridging ability could be behind the evolution of extreme SSD we experimentally induced bridging in 150 adult male and female spiders belonging to 9 different genera of diverse phylogenetic affiliation. Using independent contrasts we found that when females were small (meaning low SSD), the probability of bridging was similar for males and females, but the proportion of females that bridged significantly decreased with female body size. These results provide an additional explanation to the GH for the evolution of extreme SSD in spiders, because gravity would have an effect by reducing the bridging (not just the climbing) abilities of larger males.

24-14 Poster

THE STAMP OF SPERM COMPETITION ON THE EVOLUTION OF SEMINAL FLUID IN A BIRD

Charlie K. Cornwallis [1], Tommaso Pizzari [1]

[1] University of Oxford, Zoology, South Parks Road, OX1 3PS, Oxford, UK

charlie.cornwallis@zoo.ox.ac.uk

The research I will present examines the role of avian seminal fluid in post-copulatory sexual selection. Using artificial insemination I show in the fowl, Gallus gallus, that there are complex interactions between amount of seminal fluid inseminated and the intensity of sperm competition the donating male experienced on female promiscuity and sperm utilisation. This indicates that the volume and composition of seminal fluid transferred to females is important in determining reproductive success, which has crucial implications for our understanding of sexual selection and reproductive physiology.

24-15 Poster

BIASES IN SPERM SORTING IN A NATURAL POPULATION OF YELLOW DUNG FLIES

Marco Demont [1], Luc F. Bussière [1, 2], Claudia Buser [1], Paul I. Ward [1]

[1] University of Zurich, Zoological Museum, Winterthurerstrasse 190, 8057, Zurich, Switzerland
[2] University of Stirling, School of Biological and Environmental Sciences, FK9 4LA, Stirling, Scotland, UK

demont@gmx.ch

Over the past decade, new molecular techniques have substantially improved our knowledge of postcopulatory sexual selection (sperm competition and cryptic female choice). Nevertheless, investigations of these processes in natural populations of nonsocial insects are rare, support for ejaculate manipulation by females is still elusive, and its relevance within natural populations unknown. We genotyped sperm from the three spermathecae of wild yellow dung flies (*Scathophaga stercoraria*) caught throughout spring. Late-caught flies stored sperm from significantly more males than early-caught flies, indicating increased postcopulatory sexual selection as females aged. Furthermore, we detected significant differences amongst spermathecae in the number of ejaculates represented and a significant interaction between female size and biases in sperm storage. These findings strengthen support for considerable female control over ejaculates in this species.

24-16 Poster

INFLUENCE OF POPULATION DENSITY ON REPRODUCTIVE STRATEGIES: AN EXPERIMENT

Amélie N. Dreiss [1], Jean Clobert [2], Pierre Federici [3], Snirc Alodie [1], Julien Core [4]

[1] Université Pierre et Marie Curie - Paris 6, Laboratoire d'Ecologie, 7 quai Saint-Bernard, bat.A, 7e, case 232, 75252, Paris, France
[2] Université Paul Sabatier, Laboratoire Evolution et Diversité Biologique, 09200, Moulis, France
[3] Université Pierre et Marie Curie - Paris 6, Laboratoire d'Ecologie, Paris, France
[4] Université de Bourgogne, BioGéoSciences, Dijon, France

adreiss@snv.jussieu.fr

Population density has been predicted to affect the selective pressure on mating and reproductive behaviours. Competition for resources and mates should depend upon social context. Ultimately, fitness increasing strategies, including mate choice and sexual allocation, may therefore be different in high and low-density populations.

We tested the hypothesis that mating and reproductive strategies would be density-dependant, using in the common lizard (*Lacerta vivipara*) as our model species. We monitored female reproductive success, mate choice and offspring characteristics in experimental populations manipulated for adult density.

First results showed that the clutch sex-ratio of young females varies with density, young female producing more males in low density population. According to previous studies, these results suggest that reproductive outcomes depend on social context in this lizard species.

Key words: Density, reproductive strategies, clutch sex-ratio

24-17 Poster

GENETIC COMPATIBILITY AND FEMALE MATE CHOICE IN A LEKKING PASSERINE

Emily H. DuVal [1], Bart Kempenaers [1]

[1] *Max Planck Institute for Ornithology, Behavioral Ecology and Evolutionary Genetics, Postfach 1564, Haus nr. 5, 82319, Seewiesen, Germany*

ehduval@gmail.com

Though both males and females may be selective in mate choice, females are generally the choosier sex. This is particularly true in lekking species in which males mate polygynously and do not participate in offspring care. In the apparent absence of direct benefits for mate choice, why are females so choosy? The genetic compatibility hypothesis suggests that females choose mates to optimize the combination of maternal and paternal alleles in offspring (non-additive genetic variants). We combined field observations with genetic analyses of paternity and relatedness to test this hypothesis in a lekking passerine, the lance-tailed manakin (Chiroxiphia lanceolata). Specifically we tested 1) whether pairwise relatedness (R) between females and actual mates was less than expected from a random model of mate choice; 2) whether distance between nest site and father's display area was related to parental R; and 3) whether offspring heterozygosity was related to survival and recruitment.

24-18 Poster

GETTING READY FOR SEX: REALLOCATION OF RESOURCES INTO MATING PERFORMANCE AND REPRODUCTIVE SUCCESS IN A SCORPIONFLY

Sierk Engels [1], Leif Engqvist [1], Klaus P. Sauer [1]

[1] *University of Bonn, Institute for Evolutionary Biology and Ecology, An der Immenburg 1, 53121, Bonn, Germany*

sengels@evolution.uni-bonn.de

One of the most important and interesting issues in evolutionary biology is the evolution and investigation of mating systems. Once individuals have reached sexual maturity they are supposed to maximize their reproductive success. The way to succeed, however, differs significantly between species and between the genders as well. In resource dependent mating systems, mating and/or reproductive success are highly dependent on the individual's ability to gain access to the relevant resources. However, in some insect species individuals are able to reallocate somatic resources and use them to increase their reproductive potential, thereby becoming somewhat independent from external nutritional supply. In a previous study starving male *Panorpa vulgaris* showed a significant decrease in body mass, while their salivary glands (essential for salivary gift production) were still growing. Moreover, males and females seem to suffer a reduction in flight ability when ageing. Based on these findings we conducted an experiment testing the hypothesis that male and female *P. vulgaris* are able to histolize their flight muscles in order to reallocate these resources into reproduction (males: saliva production, females: egg production). We created different food regimes and age-groups to detect possible effects on reallocation patterns. Our preliminary analyses indicate that *P. vulgaris* scorpionflies can use somatic stored resources to improve their reproductive performance. To what extent these reallocation processes take place seems to depend on the amount of food available and on the individual's age.

24-19 Poster

INVESTIGATION OF THE BENEFITS TO MALES OF TRANSFERRING EJACULATE SEX PEPTIDE IN FRUITFLIES.

Claudia Fricke [1], Stuart Wigby [2], Tracey Chapman [1]

[1] *University of East Anglia, School of Biological Sciences, NR4 7TJ, Norwich, UK*
[2] *University College London, Department of Biology, Darvwin Building, Gower Street, WC1E 6BT, London, UK*

C.Fricke@uea.ac.uk

Sexual conflict is an important force for shaping the evolution of reproductive traits. The occurrence and intensity of sexual conflict is determined by four factors: the benefits to males of male manipulation, the costs to females of male manipulation, the benefits to females of female resistance and the costs to males of female resistance. Our analysis of the primary literature reveals that the costs to females of male manipulation have been widely studied, however, perhaps surprisingly, empirical estimates of the benefits to males of manipulating females are lacking. To address this, we performed a set of experiments to establish the benefits to *Drosophila melanogaster* males of transferring the ejaculate sex peptide during mating. Sex peptide is one of the 80 or so accessory gland proteins that males produce and transfer during mating in their ejaculates. It causes an increase in oviposition and a decrease in female receptivity to mating and is also known to increase female mortality, i.e. to be a major component of the cost of mating in female fruitflies. We conducted experiments where females were confined with males that produced or did not produce the sex peptide. We measured the sperm competitive ability of SP lacking and control males when they were the first or second males to mate with a female in tests in which matings were observed. In addition, we measured the competitive lifetime reproductive success of the same males over two weeks. The results therefore show the benefits of SP transfer in terms of number of offspring produced, in low and high competitive situations.

24-20 Poster

SPERM COMPETITION AND THE EVOLUTION OF POLYANDRY: VARIATION IN MALE GENETIC QUALITY AND ITS IMPLICATIONS FOR THE GOOD SPERM HYPOTHESIS.

Francisco Garcia-Gonzalez [1]

[1] *University of Western Australia, Centre for Evolutionary Biology, School of Animal Biology, UWA, 6009, Nedlands, Perth, Australia*

pgarcia@cyllene.uwa.edu.au

A number of genetic benefits have been proposed to explain the adaptive significance of polyandry (females mating with multiple partners in the same reproductive cycle). Intrinsic male quality hypotheses propose that polyandrous females can increase the probability that their eggs are fertilized by males of superior genetic quality. These hypotheses can be divided in those involving pre-copulatory mechanisms of sexual selection or post-copulatory mechanisms (cryptic female choice and sperm competition). Among the latest group, the good sperm hypothesis suggests that polyandrous females will accrue genetic quality for their offspring through facilitation of sperm competition if males achieving higher fertilization success are also more effective in producing viable offspring. Thus, the validity of the good sperm hypothesis relies on empirical support for a positive relationship between sperm competitiveness and offspring performance. Here I revise the implications that variation in male genetic quality may have for our ability to test this prediction. Different scenarios for the relationship between a male's ability to win fertilizations in sperm competitive contexts and his ability to induce offspring viability are simulated. The analysis highlights some issues that may lead to confusion when assessing good sperm processes.

24-21 Poster

MATERNAL ALLOCATION OF RESOURCES INTO THE EGGS IN RELATION TO PARTNER SIZE IN THE PIPEFISH SYNGNATHUS TYPHLE (L).

Inês Braga Gonçalves [1], Lotta Kvarnemo [1], Kenyon B. Mobley [2], Ingrid Ahnesjö [3], Gry Sagebakken [1]

[1] *Göteborg University, Department of Zoology, Box 463, 405 30, Göteborg, Sweden*
[2] *Texas A&M University, Department of Biology, 3258 TAMU, College Station, TX 77843, Texas, USA*
[3] *Uppsala University, Department of Animal Ecology, Norbyvägen 18 D, 752 36, Uppsala, Sweden*

ines.goncalves@zool.gu.se

Animals that reproduce more than once are expected to make adaptive decisions on how much to invest in each reproductive event. According to the Differential Allocation hypothesis, organisms should weigh the costs and benefits of investing into reproduction when mating with their current partner against the possibility of finding higher quality mates in the future. In the pipefish *Syngnathus typhle*, males care for the young in a brood pouch. Both sexes prefer large-sized mates, generating a size assortative mating pattern. Females are polyandrous and hence commonly transfer eggs to several males during each breeding season. Large males produce larger offspring than small males do, but it is unknown whether this is due solely to large males gaining access to larger females, which produce larger eggs, or if it is generated (or reinforced) by females investing more into their eggs when mating with a large male. Conversely, females might invest more into the eggs when having to mate with a small male, especially if such males provide poorer care to the eggs than large males do. This study assessed whether females show differential allocation, and whether they allocate more or less resources to the eggs, depending on the size of their mate. We let each female mate with a large and a small male, and measured diameter, weight, lipid and protein content of the eggs. Our results show that females did not invest more into the eggs when mating with a large male. Instead, the egg protein content was higher when females mated with small males, indicating a compensatory differential allocation.

24-22 Poster

FEMALE SEXUAL POLYMORPHISM AND FECUNDITY CONSEQUENCES OF MALE MATING HARASSMENT IN THE WILD

Thomas P. Gosden [1], Erik I. Svensson [1]

[1] *Lund University, Animal Ecology, Ecology Building, 223 62, Lund, Sweden*

Thomas.Gosden@zooekol.lu.se

Theoretical models suggest that the type and degree of genetic variation in female resistance could affect the evolutionary outcome of sexually antagonistic mating interactions, resulting in either rapid development of reproductive isolation and speciation or genetic clustering and female sexual polymorphisms. Laboratory studies on model organisms such as *Drosophila* have revealed genetic and phenotypic variation in female response towards male mating attempts and demonstrated sexually antagonistic co-evolution driven by mating costs on female fitness. However, there is very limited evidence for genetic variation of this kind in natural populations of non-model organisms. Likewise, we lack knowledge on female fecundity-consequences of matings and the degree of male mating harassment in natural settings. Here we present such data from natural populations of a colour polymorphic damselfly (*Ischnura elegans*). Using a novel experimental technique of colour dusting males in the field, we show that heritable female colour morphs differ in their propensity to accept male mating attempts. These morphs also differ in their degree of resistance towards male mating attempts, the number of realized matings and in their fecundity-tolerance to matings and mating attempts. These results show that there may be genetic variation in both resistance and tolerance to male mating attempts (fitness consequences of matings) in natural populations, similar to the situation in plant-pathogen resistance systems. Male mating harassment could promote the maintenance of a sexual mating polymorphism in females, one of few empirical examples of sympatric genetic clusters maintained by sexual conflict.

24-23 Poster

SEXUAL CONFLICT IN MOUTHBROODING CICHLIDS

Marcel P. Haesler [1, 2], Michael Taborsky [1]

[1] *University of Bern, Department of Behavioral Ecology, Wohlenstrasse 50a, 3032, Hinterkappelen, Switzerland*
[2] *University of Plymouth, School of Biological Sciences, Drake Circus, Plymouth, UK*

marcel.haesler@esh.unibe.ch

Multiple mating in animals is the rule rather than the exception. Nevertheless, the effect of multiple mating on sexual selection and speciation in rapidly radiating species flocks has been hitherto neglected. We studied causes and effects of multiple mating in a lekking mouthbrooding cichlid from Lake Tanganyika, *Ophthalmotilapia ventralis*. Results show that (1) sperm competition from successive spawnings occurs in the buccal cavity of the females, where the eggs are fertilized; specific mor-phological and physiological adaptations in the male reproductive apparatus enable prolonged sperm survival despite the osmotic stress caused by the contact with freshwater; (2) females collect sperm from different males even without releasing eggs, which may force males to economize on ejaculate release; and (3) predators and other competitors can strongly influence a female's decision to mate; it can even increase a female's propensity to mate multiply. These observations reveal a substantial sexual conflict in this species, which may strongly affect sexual selection and can even weaken its effects. This has implications on our understanding of speci-ation in the cichlids of the Great Lakes of East Africa, where evidence exists that sexual selection is a major force of speciation.

24-24 Poster

THE ROLE OF DIFFERENTIAL ALLOCATION IN THE REPRODUCTIVE ISOLATION OF A THREESPINE STICKLEBACK SPECIES PAIR

Megan L. Head [1], Jenny W. Boughman [1]

[1] *University of Wisconsin, Department of Zoology, 430 Lincoln Dr, 53706, Madison, USA*

head@wisc.edu

With burgeoning interest in sexual selection in recent decades it is being realized that this evolutionary process is likely to play an important role in speciation. An important aspect of sexual selection that has received little attention with regard to speciation is post-copulatory mate choice. In species with parental care post-copulatory mate choice in the form of differential allocation may be important in maintaining reproductive isolation in species where pre-mating isolation is incomplete. Differential allocation theory predicts that individuals will optimize investment in current and future reproduction according to the fitness value of each. In the context of speciation, this means that parents should invest more in offspring produced by conspecific matings than those produced by heterospecific matings. Here, I present an experiment that investigates the role of differential allocation in the reproductive isolation of limnetic/benthic species pairs of threespine sticklebacks. I discuss how male's trade-off caring for current offspring with further mate attraction, and how this affects male fitness. My results show that differential allocation can enhance premating reproductive isolation, because hybrid offspring receive less care and hence have lower fitness than predicted from genetic incompatibility alone.

24-25 Poster

HETEROSPECIFIC MATE PREFERENCES IN GROUND-HOPPERS AND THEIR ECOLOGICAL CONSEQUENCES

Axel Hochkirch [1], Julia Gröning [1]

[1] *University of Osnabrück, Department of Biology/Chemistry, Barbarastr. 13, D-49076, Osnabrück, Germany*

hochkirch@biologie.uni-osnabrueck.de

Since species are often considered discrete natural units, interspecific sexual interactions (reproductive interference) are often disregarded as potential factors determining community composition. Nevertheless reproductive interference can have significant costs for species sharing similar signal channels. Interspecific sexual interactions have often been studied in the context of hybrid zones or invasive species, but non-hybridizing species with broadly overlapping geographic ranges received less attention. We combined laboratory and field experiments with field surveys to test whether the coexistence of two congeneric ground-hopper species with overlapping ranges might be influenced by sexual interactions. The number of conspecific matings of *Tetrix ceperoi* decreased substantially in the presence of *Tetrix subulata*. Males of *T. ceperoi* performed more mating attempts with heterospecific females, whereas females of *T. subulata* rejected these more often than conspecifics. Although no heterospecific matings occurred in the laboratory, the reproductive success of *T. ceperoi* was reduced substantially in field experiments. In the field, the pattern of reproductive interference was strongly correlated with encounter frequencies, which strongly depended on the dispersion. As *T. ceperoi* occurred in strong aggregations and had stronger preferences for bare ground, the number of heterospecific encounters was reduced in this species. *T. subulata* had a broader niche and also occurred in areas where *T. ceperoi* was missing. Our results show that reproductive interference might have similar consequences as competition, such as demographic displacement of one species or habitat partitioning. Several ecological and evolutionary mechanisms might reduce the costs of reproductive interference in the field, such as ecological or reproductive character displacement.

24-26 Poster

HOW DOES TESTOSTERONE AFFECT PERFORMANCE IN THE DIFFERENT COLOUR MORPHS OF THE DALMATIAN WALL LIZARD?

Katleen Huyghe [1], Jerry F. Husak [2], Anthony Herrel [1], Raoul Van Damme [1]

[1] *Univ. of Antwerp, Dept. Biology, Universiteitsplein 1, 2610, Antwerp, Belgium*
[2] *Univ. of Massachusetts, Dept. Biology, MA 01003, Amherst, USA*

katleen.huyghe@ua.ac.be

Circulating testosterone (T) levels are mediators of aggressive displays and behaviours in a reproductive context, through their direct action on behaviour, and through their influence on morphology and performance. T levels also affect the degree of parasite infection, through their effects on immunocompetence. We tested these ideas on a population of lizards, which exhibits a colour polymorphism. Males occur in 3 different colours (white, yellow, orange), providing an opportunity to test the idea of morphs being alternative solutions to the evolutionary challenges posed on the link between hormones, morphology, performance, and parasite load. Morphs differ in size, and bite force capacity, but they don't differ in locomotion performance or activity pattern. Here, we test the hypothesis that these differences are related to differences in testosterone levels and parasite loads between morphs, suggesting a balance between different fitness effects. Secondly we test the existence of a correlation between T and different performance variables. We found that higher T levels increase bite force capacity and that the orange morph indeed has a higher blood plasma T level than the yellow morph, and that it suffers more from parasite (mite) infection. It seems that selection pressures have indeed induced alternative solutions in this species, reflected in different morphs.

24-27 Poster

GOOD GENES DRIVE FEMALE CHOICE FOR MATING PARTNERS IN THE LEK-BREEDING EUROPEAN TREE FROG

Julie Jaquiéry [1], Thomas Broquet [1], Cécile Aguilar [1], Guillaume Evanno [1], Laura Berset-Brändli [1], Nicolas Perrin [1]

[1] *University of Lausanne, Department of Ecology & Evolution, Biophore, 1015, Lausanne, Switzerland*

julie.jaquiery@unil.ch

In lek-breeding frogs, males congregate to display through costly mating calls, while females visit choruses to choose among potential mating partners. Such species are well suited to test good-genes models of sexual selection, since males provide only genes and no paternal care to their offspring.

The calling traits of male gray tree frogs (*Hyla versicolor*) have been shown to correlate with their progeny's fitness, and to affect female preference under laboratory conditions, supporting a good-genes hypothesis (Welch et al. 1998, Science, 280:1928-1930). In natural choruses, however, male mating success appeared unaffected by calling traits, casting doubts on the effectiveness of female choice in the wild (Friedl & Klump 2005, Animal Behaviour, 70:1141-1154).

We investigated male mating success and offspring fitness in a natural population of European tree frogs *Hyla arborea*, and showed that the most attractive males (in terms of number of successful matings per calling night) produced offspring of better fitness both in terms of hatching success and larval growth rate. From our results, females are indeed able to choose better partners under natural settings, and benefit from this choice through the good genes their offspring inherit.

24-28 Poster

THE EVOLUTION AND MAINTENANCE OF POLYANDRY

Ines Klemme [1], Jana A. Eccard [2], Hannu Ylönen [3]

[1] *University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, 40014, Jyväskylä, Finland*
[2] *University of Bielefeld, Department of Animal Behaviour, P.O. Box 100131, 33501, Bielefeld, Germany*
[3] *University of Jyväskylä, Konnevesi Research Station, P.O. Box 35, 40014, Jyväskylä, Finland*

klemme@cc.jyu.fi

With an increasing focus on reproduction from the female perspective during the last decades, it became clear that the traditional concept of monogamous females must be reconsidered. Polyandry, i.e. mating with multiple males within one reproductive event, is prevalent among most taxa. There is also a growing body of evidence that females gain fitness benefits from multiple mating. However, it is often unclear whether direct benefits, indirect genetic benefits, or both contribute to this advantage, and thus, their role in the evolution and maintenance of polyandry is still not fully understood. Here, we provide a comprehensive overview of a number of field and laboratory studies on the bank vole *Myodes glareolus*, designed to examine benefits of polyandry. We provide evidence that female bank voles gain diverse mutually compatible fitness benefits associated with both benefit categories. We found that also females of species with nonresource-based mating systems, can obtain direct benefits in the form of reproductive stimulation and infanticide avoidance. Additionally, offspring of polyandrous females showed an improved genetic fitness with a significant increase in reproductive success compared to offspring of monandrous females. We discuss the potential function of these benefits as the origin and maintaining force of polyandry in this species.

24-29 Poster

A MALE SEX PHEROMONE IN THE SCORPIONFLY PANORPA GERMANICA (MECOPTERA, PANORPIDAE)

Dagmar Kock [1], Joachim Ruther [2], Klaus P. Sauer [1]

[1] *University of Bonn, Institute for Evolutionary Biology and Ecology, An der Immenburg 1, 53121, Bonn, Germany*
[2] *Free University of Berlin, Institute of Biology, Applied Zoology/AnimalEcology, Haderslebener Str. 9, 12163, Berlin, Germany*

dkock@evolution.uni-bonn.de

Based on behavioural studies the existence of male sex pheromones has long been proposed for a number of scorpionfly species. Females often respond to their conspecific males only if these have everted a genital pouch with glandular epithelium, which is assumed to be the source of volatile sex attractants. In dual choice situations females of *Panorpa germanica* showed a high preference for ‘calling’ males (males with everted genital pouch) over males that were not calling, confirming that the eversion of a male’s genital pouch is associated with the release of a male sex pheromone. Volatiles emitted by males and females were collected and chemically identified by coupled gas chromatography-mass spectrometry (GC-MS). Two aldehydes [(2*E*,6*Z*)-nona-2,6-dienal and (2*E*)-non-2-enal] were found to be characteristic of calling males and bioassays applying synthetic compounds showed the identified substances to be attractive to females. To our knowledge this is the first identification of a sex pheromone in a scorpionfly.

24-30 Poster

EFFECTIVENESS OF SEXUAL AND NATURAL SELECTION IN REMOVING MUTATIONS INDUCED WITH IONIZING RADIATION

Magdalena Konior [1], Jacek Radwan [1]

[1] *Jagiellonian University, Zoopsychology and Animal Ethology, Gronostajowa 7, 30-387, Krakow, Poland*

kon@eko.uj.edu.pl

Due to production of males, sexual populations are expected to incur a fifty percent cost in potential growth rate, comparing to populations with asexual reproduction. Theoretical models predict that sexual selection, and male-male competition can compensate for this cost by decreasing the mutation load of sexual population. This hypothesis was empirically tested only twice, and the results of the experiments were discordant. Previous experiments indicated that sexual selection can remove from population mutations induced with ionizing radiation. The aim of the experiment was the comparison of the effectiveness of the natural and sexual selection in removing induced mutations from the population. Mutations were induced by means of small doses of gamma radiation. The effects of 10 Gy and 1 Gy doses of gamma radiation on F1 generation were estimated and after that, four groups of mites from generation F1, were subjected to four different regimes, which differed in opportunity of sexual and natural selection (sexual and natural selection present; sexual selection present, natural selection absent; sexual selection absent, natural selection present; sexual and natural selection absent). After that treatment, fitness of F2 generation was evaluated, estimating main fitness components including: competitiveness of males in access to females and sperm competition, fecundity of females, survivability from egg to adult and longevity.

24-31 Poster

SEXUAL ANTAGONISM IN OFFSPRING NUMBER AND SIZE REVEALED BY NEGATIVE GENETIC CORRELATION

Esa Koskela [1], Tapio Mappes [1], Tuula A. Oksanen [1], Eero Schroderus [1]

[1] *University of Jyväskylä, Biological and Environmental Science, P.O. Box 35, FIN-40014, Jyväskylä, Finland*

emk@cc.jyu.fi

Sexually antagonistic genes are alleles that have differential fitness effects on males and females. Recognizing sexually antagonistic selection and sexually antagonistic traits is essential for understanding the evolution of central life history traits, such as offspring number and size. We addressed this issue by examining the genetic correlation between sire and dam effects for these traits in the bank vole *Myodes glareolus*. The data, based on pedigreed laboratory colony founded by wild captured individuals, contains records from 1394 litters measured at birth. Variance components were estimated with the REML-animal model procedure. In the analysis, the genetic effect of sire was fitted as an additional random effect for female litter size. The results showed that the effect of sire on litter size had a negative genetic correlation to both direct effects on offspring number and size at birth. Our study gives novel evidence for sexually antagonistic selection on central life-history traits in mammals. The results suggest that antagonistic selection between the sexes may be one factor maintaining genetic variation in the studied traits.

24-32 Poster

RESTRICTIVE MATING BY FEMALES ON BLACK GROUSE LEKS

Christophe Lebigre [1], Rauno V. Alatalo [1], Heli Siitari [1], Silja Parri [1]

[1] *University of Jyväskylä, Department of Biological and Environmental Science, PO Box 35, 40014 Jyväskylä, Finland*

lebigre@bytl.jyu.fi

In lekking species, it has long been assumed that polyandry is rare because female choice is free and male-male competition is strong. However, polyandry has been reported in most lekking species studied so far. Here we combined a parentage analysis to behavioural data to investigate the mating behaviour of black grouse females. In this species, lek observations suggest that most females mate only once, but polyandry may be underestimated if females mate outside the lek and/or on several leks. Within a restricted area around our study sites, a small proportion of matings (c. 10%) seemed to take place with males displaying solitarily. Forty percent of the copulations between males displaying on the studied leks and radio-tagged females were not recorded by us. This is probably due to difficulties in identifying the females and because our observations did not cover all the possible time for matings. Females of the undetected copulations had chosen males that were already known to be successful on the leks. When the mating partners were identified, there was a strong consistency between the observations and true paternity, even when the copulation was disturbed by a neighbouring male. Multiple mating and multiple paternities were rare. We can now confidently ascertain that most females not only mate with one male, but also mate only once for the whole clutch. This remarkable mating behaviour requires that a single insemination is sufficient to fertilize the clutch and that females can determine whether the sperm has been successfully transferred. Indeed, grouse Tetraoninae with many lekking species may be the only bird taxon that has evolved these traits.

24-33 Poster

UNDERSTANDING MATING SYSTEMS: A MATHEMATICAL MODEL OF THE PAIR FORMATION PROCESS

Aline M. Lee [1], Steinar Engen [2], Bernt-Erik Sæther [1]

[1] *Norwegian University of Science and Technology, NTNU, Department of Biology, Realfagsbygget, 7491, Trondheim, Norway*
[2] *Norwegian University of Science and Technology, NTNU, Department of Mathematical Sciences, 7491, Trondheim, Norway*

aline.lee@bio.ntnu.no

Mechanisms generating inequalities among males in reproductive success are key to understanding the evolutionary significance of sexual selection. A stochastic model for quantitatively describing and analyzing mating systems on a continuous scale from strict monogamy to extreme polygyny is presented. Effects of different mating system characteristics on the variance in mating success and on the opportunity for sexual selection are explored. The factors studied include degree of inequality among males, interdependence of mating events, population size, and sex ratio. It is also shown that different combinations of mating system characteristics can lead to the same variance in male mating success, although the distribution differs, emphasizing that the variance in reproductive success alone is not a sufficient descriptor of mating systems. An extension of this model can be used to study the effects of mating system (here also including polyandry) and age structure on lifetime reproductive success, genetic drift and sexual selection.

24-34 Poster

EVOLUTION OF COURTSHIP BEHAVIOUR IN TWO SPECIES OF OLD-WORLD FLYCATCHERS (FICEDULA HYPOLEUCA, F. ALBICOLLIS)

Gry A. Lien [1], Glenn P. Sætre [1]

[1] *University of Oslo, CEES, Department of Biology, P.O.box 1066, 0316, Oslo, Norway*

gryal@student.matnat.uio.no

Studies of female choice and male traits like plumage colour and territorial song have earlier been done on two species of flycatchers, *Ficedula hypoleuca* and *F. albicollis*. These studies have found a divergence in male plumage traits and song that reinforces premating isolation in sympatric populations. Here we present results from a pioneer study of another phenotypic trait that has not yet been the investigated, namely male courtship behaviour, to see if this trait followed the same patterns of character displacement as plumage colour and territorial song. The study involved 12 different courtship displays along with time devoted in each of three specified areas around the nestbox (distance from the nestbox). Populations investigated include The Czech Republic (both species in sympatry), Italy (allopatric population of *F. albicollis*) and Norway (allopatric population of *F. hypoleuca*). We also did recordings of the courtship song for further analyses. In the study free-living males where presented with a caged female and the sequence of displays that the males performed during a period of 10 minutes where recorded. We found that several of the behaviours showed significant differences between sympatric and allopatric populations of the two species and that especially behaviours related to nest-hole advertisement show a divergence in sympatry, i.e. the species have more different behaviours in sympatry than in allopatry.

24-35 Poster

QUANTIFYING SEXUAL SELECTION IN HERMAPHRODITES

Maria Cristina Lorenzi [1], Gabriella Sella [1]

[1] *University of Turin, Dept. of Animal and Human Biology, via Accademia Albertina 13, 10123, Turin, Italy*

cristina.lorenzi@unito.it

Experimental tests of sexual selection in hermaphrodites have been rarely accomplished and most evidence of its role is circumstantial. Simultaneous outcrossing hermaphrodites compete with each others for mating in the preferred sexual role. Under monogamy, such a conflict is evolutionarily solved by conditional reciprocity in gamete exchange. Under promiscuity, individuals increase their investments in the male sex with respect to hermaphrodites under monogamy, as predicted by sex allocation theory and do this at the expenses of the female function. As the proportion of resources invested in the two sex functions vary with mating regimes, so does sexual selection on each sex function. We evaluated the "opportunity of sexual selection" for both the female and the male function in the simultaneous, outcrossing hermaphrodite *Ophryotrocha diadema,* by measuring focal hermaphrodites' paternal and maternal offspring in replicated monogamous and promiscuous regimes, using genetic markers to estimate paternity. We document that mating regimes set up the opportunity for sexual selection on both sex functions and that, under promiscuity, hermaphrodites have higher opportunities for sexual selection both for the male and for the female function than those under a monogamous regime. We discuss the hypothesis that, under promiscuity, strong sexual selection pressures may destabilise hermaphroditism, if "functionally pure" sex strategies invade a hermaphroditic population.

24-36 Poster

MALE INBREEDING TOLERANCE WHEN AVAILABILITY OF FEMALES VARIES

Hanne Løvlie [1], Tommaso Pizzari [2]

[1] *Stockholm University, Dept. of Zoology, 10691, Stockholm, Sweden*
[2] *University of Oxford, EGI, South Parks Road, OX1 3PS, Oxford, UK*

hanne.lovlie@zoologi.su.se

Inbreeding avoidance is repeatedly reported in the animal kingdom with the adaptive explanation of avoiding inbreeding depression. However, with inbreeding comes the benefit of increased inclusive fitness. Theoretically is inbreeding tolerance therefore predicted to be typically higher than observed, particularly when little parental care is provided and availability of reproductive partners is high. Variation in male inbreeding tolerance was studied in the red junglefowl, a promiscuous species with no paternal care of offspring. Males were exposed to 'high' (four females; two sisters and two unrelated), 'intermediate' (two females; one sister and one unrelated) and 'low' availability of females (a sister and an unrelated female, available on occasions separated in time). Males under all three condidtions engaged in both incestuous and outbreed copulations, but tended to prefer unrelated females over sisters when availability to females was 'high'. On the other hand, when availability of females was reduced from 'intermediate' to 'low' males tended to allocate larger ejaculates to sisters. The results show that (i) males engage in incestuous copulations even when availability of females is relatively high, but (ii) may shift from investing in outbreed copulations to rather invest in incestuous copulations when availability of females is reduced and the relative value of an incestuous mating likely to increase.

24-37 Poster

EXPOSURE TO PESTICIDES REVEALS CONDITION-DEPENDENCE IN FISH ORNAMENTS –AND UNCOVERS A NOVEL THREAT TO NATURAL POPULATIONS

Omar Arellano-Aguilar [1], Constantino Macias Garcia [1]

[1] *Universidad Nacional Autonoma de Mexico, instituto de Ecologia, A.P. 70-275, Coyoacán, 04510, Mexico DF, Mexico*

maciasg@servidor.unam.mx

Condition-dependence, where the magnitude of an attribute accurately reflects the past condition of the organism, arises through directional selection on traits involved in attracting mating partners, and implies a disproportionate increase of production/maintenance cost of traits as they become exaggerated beyond their naturally-selected optimum. There are many demonstrations of costs of ornaments, but few convincing examples of condition-dependence. Here we show that the expression of ornaments in the viviparous Amarillo fish (*Girardinichthys multiradiatus*) is influenced by embryonic exposure to low concentrations of an organophosphorous insecticide. Male ornamental fin size, dimorphic yellow colouration and display rates were all compromised in exposed fish, but unaffected in their paternal half-sibling controls and in their sisters (only morphology and colour). Exposed males and females were smaller than controls, thus the differential effect was restricted to attributes such as fin size only above the naturally-selected magnitude shown by females. Father phenotype predicted offspring morphology, but the slope of the regression of experimental males was lower than that of the controls, further demonstrating condition-dependence of male ornaments. Since exposed males were discriminated against by both control and exposed females, this sub-lethal developmental effect can reduce the effective population size and bring natural populations closer to extinction.

24-38 Poster

SEXUAL CONFLICTS IN PLANTS: POLLEN DONOR EFFECTS ON TIMING OF STIGMA RECEPTIVITY WITHIN AND BETWEEN POPULATIONS OF COLLINSIA HETEROPHYLLA

Josefin A. Madjidian [1], Åsa Lankinen [1]

[1] *Lund University, Plant Ecology and Systematics, Ecology building, 223 62, Lund, Sweden*

josefin.madjidian@ekol.lu.se

A conflict between the sexes is believed to lead to population differentiation as male manipulative traits and female defence traits coevolve. In *Collinsia heterophylla*, an annual hermaphrodite plant with delayed stigma receptivity, we recently found, using one-donor crosses, that both recipient and donor affected the onset of stigma receptivity. The female control over its stigma receptivity is thus incomplete, which can inflict a fitness cost. This situation opens for a sexual conflict also in plants. To test the consequences of a possible sexual conflict at the population level we made crosses within and between populations. Two of the four populations used were differentiated from the other two according to a phylogenetic analysis. Preliminary data showed no significant effect of origin of either pollen or stigma on timing of stigma receptivity. When we compared crosses within and between differentiated population forms however, we found a significant interaction effect; when a recipient was pollinated with a donor of a different form, the stigma receptivity was delayed longer, compared to when pollinated with the same form. Furthermore, fertilisation by pollen of the same form resulted in less seeds at early stage. This reduction in seed production could not be found when the pollen source was of a different form. So, our preliminary data suggest that female plants were able to withstand pollen of *other* forms better, which also reduced the potential cost of lowered seed production in early stages. The results will also be discussed in relation to characteristics important for the mating system of this plant species, such as anther-stigma contact and flower size.

24-39 Poster

DIRECT AND INDIRECT FITNESS EFFECTS OF INCREASED RESISTANCE TO MATING IN A BEETLE: AN EXPERIMENTAL APPROACH

Alexei A. Maklakov [1], Göran Arnqvist [2]

[1] *The University of New South Wales, School of Biological, Earth and Environmental Sciences, Kensington, 2052, Sydney, Australia*
[2] *Uppsala University, Animal Ecology, Norbybagen 18D, 75236, Uppsala, Sweden*

A.Maklakov@unsw.edu.au

The evolution of female choice, i.e. female traits that bias fertilization success towards particular male phenotypes, is at heart of the current research on sexual selection. Indirect genetic benefits of female choice through increased fitness of the offspring have been traditionally invoked to explain the evolution of mate choice. However, recent theory suggests that direct benefits of female resistance to mating are more likely to drive the evolution of traits that determine female preference. Here we simulated the evolution of female ‘resistance’ traits by directly manipulating female phenotype to either increase or decrease female choosiness (ability to resist male harassment) in a seed beetle, *Callosobruchus chinensis*. We then estimated direct and indirect fitness benefits/costs of increased/decreased choosiness under experimental conditions that reflect recent evolutionary history of this population. First, we estimated the effect of these artificial ‘traits’ on direct female fitness in replicate subpopulations. Second, we reared offspring from all subpopulations and estimated lifetime reproductive success of sons in a competitive setting and net fecundity of daughters. We show that increased resistance to mating resulted in 33% increase in offspring production, while decreased resistance resulted in 34% decrease compared to controls. There was no significant effect of female treatment on reproductive success of either sons or daughters. Thus, the evolution of such female choice trait would considerably increase female fitness, yet have no discernible effect on mating success of the sons or fecundity of the daughters. These results suggest that direct benefits of increased resistance to mating are likely to drive the evolution of female preferences in this system.

24-40 Poster

WEAK INTERSEXUAL FITNESS CORRELATION FOR STANDING GENETIC VARIATION AND NEW MUTATIONS; IMPLICATIONS FOR SEXUAL SELECTION

Martin A. Mallet [1], Adam K. Chippindale [1]

[1] *Queen's University, Biology, BioSciences Complex, K7L 3N6, Kingston, Canada*

malletm@biology.queensu.ca

Empirical studies of naturally-occurring fitness variation are rare because the direct measurement of total fitness is challenging; quantitative studies of Darwinian fitness require simultaneous control over environmental and genetic factors affecting an organism’s life. Laboratory-adapted populations can be used to overcome these difficulties because their well-defined lifecycles and available genetic tools make fitness directly measurable. Using a population of Drosophila melanogaster adapting to laboratory conditions since 1975, we are directly measuring factors that contribute to the maintenance of total fitness variation using hemiclone analysis. This method allows us to isolate near-complete haploid genomes and directly measure their phenotypic consequences in each sex. Preliminary results indicate that males do not exhibit greater genetic variance for net fitness than females and that the intersexual correlation for total fitness is near-zero, diminishing the genetic benefits of sexual selection. However, pilot studies using mutation-accumulation lines suggest that males suffer the effects of mutation to a much greater extent than females, in accordance with some theories of the maintenance of sexual reproduction by sexual selection. Whether this effect can overcome the weak intersexual correlation found is the subject of further investigation.

24-41 Poster

SEXUALLY ANTAGONISTIC GENES FOR REPRODUCTIVE SUCCESS IN THE BANK VOLE, CLETHRIONOMYS GLAREOLUS

Suzanne C. Mills [1], Esa Koskela [2], Tapio Mappes [2]

[1] *UMR 5244-CNRS-EPHE-UPVD, Biologie et Ecologie Tropicale et Méditerranéenne, Université de Perpignan Via Domitia, 66860, Perpignan, France*
[2] *University of Jyväskylä, Biological and Environmental Science, P.O Box 35 YAC, FIN-40014, Jyväskylä, Finland*

mills@sooozie.co.uk

'Good genes' models of sexual selection hypothesise that in the absence of direct benefits, females receive indirect genetic benefits via offspring fitness. However, these models may be complicated by the presence of sexually antagonistic genes. Such alleles are expressed by males and females, but cause a negative intersexual correlation for fitness, therefore, 'good genes' may be highly gender specific in terms of offspring fitness.

We created selection lines divergent for the main determinant of male mating and reproductive success in the polygynandrous bank vole; testosterone (High and Low T; females based on mean T levels of their brothers). Homozygous (male x female crosses: High x High T or Low x Low T) and heterozygous (High x Low T) selection lines were produced. We measured the reproductive success of 294 pups from 76 litters. Female reproductive success was determined from female-female competition for a sexually active male; male reproductive success was determined using two measures: male-male competition for an oestrus female and microsatellite paternity analyses following mating trials.

Our results reveal significant negative intersexual correlation for reproductive success using brother-sister averages within each litter, but only for litters from homozygous selection lines. Female bank voles may therefore need to use sperm of different males to optimise the fitness of their sons and daughters and in this way, genetic variation for sexually selected traits will be maintained.

24-42 Poster

SEXUALLY ANTAGONISTIC SELECTION LINES: DO FEMALES PRODUCE LITTERS WITH AN OPTIMAL SEX RATIO?

Mikael P. Mokkonen [1], Esa Koskela [1], Tapio Mappes [1], Suzanne C. Mills [2]

[1] *University of Jyväskylä, Department of Biological and Environmental Science, PO Box 35 (YA), 40014, Jyväskylä, Finland*
[2] *Université de Perpignan Via Domitia, Biologie et Ecologie Tropicale et Mediterranéenne, UMR 5244-CNRS-EPHE-UPVD, 66860, Perpignan, France*

mimokkon@bytl.jyu.fi

Sexual antagonism between males and females may potentially exert profound effects on the reproduction of a species. Previous studies have shown that litters can be influenced by both genetic and (*in utero*) environmental effects before birth. In bank voles (*Myodes glareolus*), sex ratios range from all male to all female litters, from approximately 1 to 8 pups per litter. We created divergent selection lines according to sexually antagonistic effects. In the "high quality female" line (QuFe), we selected for families that were expected to produce high quality female and low quality male pups. The "high quality male" line (QuMa) was selected for the opposite pattern (high quality male and low quality female pups). Female quality was assessed by female-female competition for a sexually active male and male quality was based on male-male competition for a female in estrus. Here we tested the hypothesis that mothers from QuFe lines should allocate more to female pups and the mothers from QuMa lines should allocate more to male pups. Physiological measures as well as litter characteristics were analyzed. Our results indicate that mothers might optimize the sex ratio of their litters according to the quality of male and female pups. Valuable insight into sexual antagonism, the quality of individuals and the uterine environment can be gained from studying litters, which can all bring more clarity to the maintenance of genetic variation.

24-43 Poster

ASSESSING THE EXTENT OF GENOME-WIDE INTRALOCUS SEXUAL CONFLICT VIA EXPERIMENTALLY ENFORCED GENDER-LIMITED SELECTION

Edward H. Morrow [1], Andrew D. Stewart [2], William R. Rice [2]

[1] *Uppsala Universitet, Ecology and Evolution, Norbyvägen 18D, 75236, Uppsala, Sweden*
[2] *UCSB, Ecology, Evolution and Marine Biology, 93110, Santa Barbara, USA*

ted.morrow@ebc.uu.se

Intralocus sexual conflict, which occurs when a trait is selected in opposite directions in the two sexes, is a taxonomically widespread phenomenon. The strongest genetic evidence for a gender load due to intralocus sexual conflict comes from the *Drosophila melanogaster* laboratory model system, in which a negative genetic correlation between male and female lifetime fitness has been observed. Here, using a *D. melanogaster* model system, we utilize a novel modification of the 'middle class neighborhood' design to relax selection in one sex, while maintaining selection in the other. After 26 generations of asymmetrical selection, we observed the expected drop in fitness of the non-selected sex compared to that of the selected sex, consistent with previous studies of intralocus sexual conflict in this species. However, the fitness of both sexes, whether selected or not, rapidly declined compared to the base population. This overall decline in fitness indicates that the gender load of our population, due to segregating sexually antagonistic alleles, is smaller than the mutational load, due to unconditionally deleterious mutations. In addition, our assay provides an empirical demonstration of a substantial mutational load within our population.

24-44 Poster

SEX PHEROMONES, HORMONES AND BEHAVIOUR DURING THE REPRODUCTION OF CYPRINID FISH

Håkan Olsén [1]

[1] *Södertörn university college, Life Sciences, Sweden*

hakan.olsen@sh.se

As in mammals, fish sex pheromones can induce rapid behavioural (*releaser*) responses, or slower physiological (*primer*) effects such as increased hormone levels. Communication with chemical signals is probably one of the most important sources in the aquatic environment concerning information about reproductive status of the opposite sex but odours may also carry information about species identity (by definition pheromones) to avoid interbreeding. The goldfish (*Carassius auratus*) is one of the most studied vertebrates concerning sex pheromone function. During their preovulatory luteinizing hormone (LH) surge, female goldfish release pheromonal steroids that increase male LH and milt (sperm and seminal fluid) prior to spawning and, after ovulating, they release pheromonal prostaglandins that trigger male sex behavior and further elevate LH. To develope a model fish species to investigate hormonally derived pheromones under natural conditions, we study the crucian carp (*Carassius carassius*). Our initial studies used electro-olfactogram (EOG) recording to demonstrate that the olfactory epithelium of crucian carp is very sensitive to the same steroids and prostaglandins as the goldfish and exposing male crucian carp to the oocyte maturation-inducing steroid 17α,20β-dihydroxy-4-pregnen-3-one (17,20β-P) increases LH concentration, thereby increasing their milt. Most recently, field studies demonstrated that exposure to ovulatory female crucian carp increases male LH and milt, but also that these effects are mimicked by exposure to nonovulatory, 17,20ßP-injected females, indicating goldfish and crucian carp employ a homologous preovulatory hormonal pheromone. This study, *the first to document activity of a hormonally derived pheromone in wild fish in natural waters,* indicates that similar studies are practical in other Swedish cyprinids. The next step in the project will be to investigate if hormonally-derived pheromones are present in commonly occurring sympatric cyprinid species.

24-45 Poster

SEXUAL SELECTION FOR GENETIC QUALITY OF THE MALE: FEMALE CHOICE OR COMPETITION BETWEEN MALES?

Nina Pekkala [1], Mikael Puurtinen [1], Janne S. Kotiaho [1]

[1] *University of Jyväskylä, Department of Biological and Environmental Sciences, P.O. Box 35, FIN-40014, University of Jyväskylä, Finland*

nianpekk@cc.jyu.fi

The good genes theory of sexual selection emphasizes the role of females in choosing males of high genetic quality. However, better mating success of high quality males can also be brought about by competition between males. In this study, we tested the relative importance of female choice and competition between males in *Drosophila montana* fruit flies. We manipulated genetic quality by inducing mutations using gamma radiation, and examined the effects of inherited mutations on the mating success and courtship behavior of the F_1 males. In order to determine the relative importance of female choice and competition between males in sexual selection, we carried out two experiments. In the first experiment only one male was introduced to a female; in the second experiment two males were simultaneously introduced to a female. The inherited mutations reduced male's willingness to court the female, but no evidence of female choice was found. Our results suggest that sexual selection for high genetic quality can be mediated by competition between males. Competition between males should thus be more carefully considered in future research on sexual selection for genetic quality.

24-46 Poster

EVIDENCE FOR A SIGNALING FUNCTION FOR THE CONSUMED SPERMATOPHORES OF A LADYBIRD BEETLE

Jennifer C. Perry [1], Locke Rowe [1]

[1] *University of Toronto, Department of Ecology and Evolutionary Biology, 25 Harbord St, M5S3G5, Toronto, Canada*

jperry@zoo.utoronto.ca

In many insects, males provide edible material to females before or after copulation (a ‘nuptual gift’). Gifts of seminal material are particularly intriguing because the effects of ejaculate proteins often seem detrimental to female fitness. We hypothesize that seminal gifts will induce the same kinds of changes in females that seminal proteins do when transferred to the reproductive tract: increased oviposition, shorter lifespan, and reduced mating receptivity. Females of the two-spot ladybird beetle (*Adalia bipunctata*; Coleoptera: Coccinellidae) normally eject and consume the spermatophore after mating. We manipulated spermatophore consumption (allowing or preventing spermatophore feeding) of females assigned to low, medium or high nutrient condition. We predicted that if spermatophores function as a food source, then low-food females shoud respond most strongly to spermatophore feeding; if spermatophores have a signalling function, however, the effect of spermatophore feeding should be similar across food treatments. Eating a spermatophore caused females to oviposit sooner than if they did not eat a spermatophore, and this effect did not depend on female diet. The other responses tested – fecundity, egg fertility, egg mass, resistance to re-mating and longevity – were not affected by spermatophore feeding. These results indicate that spermatophore feeding transfers a signal to females and that spermatophores provide little, if any, nutritional value.

24-47 Poster

INDIVIDUAL MALE MATING PREFERENCES IN A LAKE VICTORIA CICHLID FISH: A ROLE FOR SEX RATIO SELECTION?

Michele E. R. Pierotti [1], Ole Seehausen [1, 2]

[1] *University of Berne, Aquatic Ecology and Macroevolution, Baltzerstrasse 6, CCH - 3012, Berne, Switzerland*
[2] *EAWAG, Fish Ecology and Evolution, Seestrasse 79, CH - 6047, Kastanienbaum, Switzerland*

michele.pierotti@eawag.ch

Sexual selection theory rests on the assumption that there is individual variation in mating preferences and that individuals are consistent in their preferences. However, empirical studies of within-population variation in mating preferences have received limited attention and only rarely wild individuals have been tested. We studied a colour polymorphic population of the Lake Victoria cichlid fish *Neochromis omnicaeruleus* and assessed individual variation in male mating preferences for the three female colour morphs. We tested individual wild males multiple times in three-way choice trials and found extreme individual variation in the consistency and direction of male mating preferences for female colour morphs. In this species, female colour polymorphism is associated with the presence/absence of sex ratio distorters. We thus tested the hypothesis that male mating preference variation has evolved in response to sex ratio selection to avoid matings generating sex biased clutches. The prediction is that matings with females of the preferred colour morph should produce more even offspring sex ratios than matings with non-preferred female colour morphs. Males individually characterised for their preferences were mated with multiple females belonging to both the preferred and the non-preferred colour morph and sex and colour of the offspring were recorded. We discuss the relevance of our results on within-population variation in male mating preferences and the effects of sex ratio selection in view of recent models of sympatric speciation by mutual mate choice and sex ratio selection.

24-48 Poster

DIRECT AND INDIRECT EFFECTS OF SEXUAL CONFLICT IN GUPPIES (POECILIA RETICULATA)

Clelia Gasparini [1], Alessandro Devigili [1], Virginia F. P. Da Cunha [2], Andrea Pilastro [1]

[1] *University of Padova, Department of Biology, via Ugo Bassi 58/B, 35131, Padova, Italy*
[2] *University of Aveiro, Department of Biology, Aveiro, Portugal*

andrea.pilastro@unipd.it

We investigated the effect of sexual conflict on female life–time fecundity in the guppy (*Poecilia reticulata*), of livebearing fish in which males can forcibly inseminate females through gonopodial thrusts. Two groups of females were exposed to low sexual conflict (LSC, 3 males for 1 day) or high sexual conflict (HSC, 3 males for 8 days) during each breeding cycle, and monitored for the following 10 broods. Whereas sexual conflict did not affect female mortality and overall life–time fecundity, HSC females produced more offspring early in life and fewer offspring later, as compared to their LSC counterparts. Male offspring phenotype at maturity was measured on offspring raised from brood #4. Using a mixed model MANOVA, we found that HSC females produced sons with relatively higher sperm reserves, lower courtship rate, higher gonopodial thrust rate and shorter gonopodium as compared to the sons of LSC females, suggesting that sexual conflict may have indirect effects on traits subject to pre- and post-copulatory sexual selection.

24-49 Poster

SPECIES RECOGNITION CAN EXPLAIN THE DIRECTION OF FEMALE MATE PREFERENCES IN THE GRASSHOPPER CHORTHIPPUS BIGUTTULUS

Klaus Reinhold [1], Kamran Safi [2], Jakob Heinzle [3]

[1] *University Bielefeld, Evolutionary Biology, Morgenbreede 45, D-33615, Bielefeld, Germany*
[2] *University of Zurich, Zoological Institute, Winterthurerstr. 190, CH-8057, Zurich, Switzerland*
[3] *University/ ETH Zurich, Institute of Neuroinformatics, Winterthurerstr. 190, CH-8057, Zurich, Switzerland*

Klaus.Reinhold@uni-bielefeld.de

Species recognition and intraspecific mating preferences constitute two basic aspects of animal communication. Both can be considered as variations in response to signals and they have been suggested to represent a continuum. Selection on species recognition could therefore influence intraspecific mating preferences. We examined whether females of the grasshopper *Chorthippus biguttulus* prefer conspecific male signals that can be distinguished more reliably from sympatrically occurring heterospecific signals. To evaluate the difference between songs, we extracted song parameters from the songs of 100 males of *Chorthippus biguttulus* and from heterospecific males of 10 other species using a Fourrier-Transformation. In a next step we reduced the dimensions of our data set from the received 2000 FFT components to 20 using a Principal Component Analysis. An analysis of the received data set showed that the songs of attractive males are more different from heterospecific signals than the songs of less attractive males. Our results show that females of the grasshopper *Chorthippus biguttulus* prefer conspecific male signals that can be distinguished more reliably from sympatrically occurring heterospecific signals. These results suggest that intraspecific sexual selection is influenced by pleiotropic effects from species recognition in *C. biguttulus*.

24-50 Poster

UV AND RED SIGNALS ARE BOTH IMPORTANT IN STICKLEBACK MATE CHOICE

Ingolf P. Rick [1], Theo C. M. Bakker [1]

[1] *University of Bonn, Institute for Evolutionary Biology and Ecology, An der Immenburg 1, 53121, Bonn, Germany*

irick@evolution.uni-bonn.de

Numerous studies on visual signaling in animals have focused on the role of ultraviolet (UV) wavelengths. The three-spined stickleback, a species showing distinct visually guided behaviour, uses UV wavelengths in intraspecific interactions. Given that UV-reflectance patterns are only one part of stickleback male breeding coloration, we compared the UV waveband with other wavebands located in the human visible range between 400 and 700nm. We did this by observing the response of female sticklebacks to the removal of male UV reflectance compared to the removal of three other wavebands. In detail, a female could choose between four males whose appearance was manipulated using filters, which blocked single parts of the stickleback visible spectrum corresponding closely to the spectral sensitivity of each of the four cone types. Thus, four male visual appearances were constructed, one without UV (UV-), one without short wavelengths (SW-), one without medium wavelengths (MW-) and one without long wavelengths (LW-). Females preferred SW- and MW- males, whereas UV- and LW- males were least preferred, suggesting that female sticklebacks show the greatest response to the removal of very short and very long wavelengths. Thus, we could demonstrate that UV signals are of special relevance in this species, apparently operating in combination with signals of longer wavelength reflectance like the red throat coloration. Finally, we present some data on receptor modeling by assessing quantum catches of the four stickleback cone types viewing different male body regions for each light treatment and calculating discriminability between body regions and the experimental background.

24-51 Poster

THE EFFECTS OF TESTOSTERONE AND CONDITION MANIPULATION DURING MOULT ON PLUMAGE AND IMMUNITY IN THE BLUE TIT (CYANISTES CAERULEUS).

Mark L. Roberts [1], Anne Peters [1]

[1] *Max Planck Institute for Ornithology, Vogelwarte Radolfzell, schlossallee 2, 78315, Radolfzell, Germany*

roberts@orn.mpg.de

The immunocompetence handicap hypothesis suggests that testosterone has a dual effect of increasing male sexual signal expression while concomitantly having a suppressive effect on the immune system; so only males in good condition can afford to possess high enough levels of the hormone to fully express their epigamic traits without compromising their immunity. In this study we manipulated testosterone and body condition (by using implants and different dietary regimes, respectively) in moulting blue tits to ascertain whether the hormone affects subsequent plumage colouration; whether this effect is mediated by condition; and whether testosterone and condition affect immunocompetence. We found that testosterone treatment had no effect on plumage characteristics measured immediately after the moult, but did have a positive effect on crown ultraviolet reflectance during the following breeding season. Previous studies have found evidence to suggest that this plumage characteristic is important in sexual signalling in this species, as crown UV reflectance is higher in males than females. We also found that testosterone treatment increased antibody response in moulting males, but only in those males that were in relatively poor condition. We therefore found no immunosuppressive cost associated with elevated testosterone during the moult, but also no immediate positive effect of the hormone on plumage characteristics. These results suggest that testosterone does not have an immediate effect on sexually selected plumage development in this species, but does have an eventual, positive effect during the breeding season. We also report the results of immune tests carried out during the breeding season when a difference in crown UV between testosterone treatment groups was found. We discuss these results in the context of the immunocompetence handicap hypothesis.

24-52 Poster

TRADE-OFFS BETWEEN COMPONENTS OF FITNESS AND SEXUALLY ANTAGONISTIC SELECTION MAINTAIN VARIANCE IN UNGULATE WEAPONRY

Matthew R. Robinson [1], Loeske E. B. Kruuk [1]

[1] *The University of Edinburgh, Institute of Evolutionary Biology, King's Buildings Campus, West Mains Road, EH10 4QY, Edinburgh, United Kingdom*

matthew.r.robinson@ed.ac.uk

In order to understand the evolution of a secondary sexual trait we need to examine both the selection pressures to which it is subject, via either reproductive success or viability, and its genetic basis. An elegant theoretical framework exists with which to quantify selection pressure on phenotypic traits, but selection rarely acts upon only a single trait in isolation, in only one sex, or consistently throughout life. Similarly, the maintenance of genetic variance in the presence of directional selection has been a central issue in sexual selection theory, but it is becoming increasingly apparent that estimates of single trait heritabilities may have little predictive power in the presence of genetic covariance with other important traits, for example expressed in the opposite sex, or if genetic expression varies with age. We combine new analytical approaches with an extensive long-term data set to test these issues within a wild population of Soay sheep (*Ovis aries)*, where both males and females produce weaponry in the form of horns. By using life-history data and accounting for environmental variation and covariance with other traits, we show that sexually antagonistic selection and trade-offs between reproductive success and survival may maintain variation in weaponry within this population. Furthermore using the ‘animal model’, a quantitative genetic analysis developed by animal breeders, we use multi-generational pedigree data to examine the patterns of genetic covariance in horn size between the sexes and with other traits. The combination of these two approaches allows us to examine the potential constraints on the evolution of a secondary sexual trait.

24-53 Poster

AN HEMICLONAL ANALYSIS OF THE GENIC CAPTURE HYPOTHESIS

Nicolas O. Rode [1], Edward H. Morrow [1]

[1] *Uppsala University, Animal ecology, Norbyvägen 18D, 75236, Uppsala, Sweden*

nicolas.rode@ens-lyon.fr

Additive genetic variance for fitness-related traits is predicted to be low, according to the lek paradox. The “genic capture hypothesis” explains the maintenance of genetic variation in these traits, assuming a condition dependence of such traits and a high genetic variation for condition. The former assumption has been widely investigated; however, little is known about the validity of the latter. In this study, we investigated standing genetic variation for condition and fitness in Drosophila melanogaster males. We address three questions relevant to this topic: 1/ Is there genetic variation for condition in D. melanogaster males? 2/ Is there a genotype x environment interaction (which could explain the standing genetic variation for condition)? 3/ Are condition and fitness genetically correlated? Additive genetic variance for condition and fitness were calculated using a hemiclonal analysis. Individuals of a hemiclone line share the same copy of a single haplotype. The absolute fat content across 15 hemiclone lines was used as an index of body condition and measured on flies reared in two environments (High vs Low larval density). Adult male fitness was determined through a competition experiment with genetically marked (LHM-bw-) competitor males. The relative fitness of the hemiclones was calculated as the deviation between the actual and expected reproductive success.

24-54 Poster

DOES INTERSEXUAL COEVOLUTION CAUSE RAPID POPULATION DIVERGENCE? EVIDENCE FROM POPULATION CROSSES AND THE DROSOPHILA TRANSCRIPTOME.

Mark A. Rogers [1], Adam Chippindale [1]

[1] *Queens University, Biology, 116 Barrie Street, K7L3NK, Kingston, Canada*

rogersm@biology.queensu.ca

In recent years both theory and empirical data have suggested that male and female evolution is intrinsically linked and may be characterized by open-ended cycles of adaptation and counter-adaptation. Studies showing that genes involved in reproduction tend to evolve rapidly relative to the rest of the genome lend credence to this theory and implicate intersexual co-evolution as an important mechanism of population divergence. To study this phenomenon, our lab is using a model phylogeny of *Drosophila* populations which diverged from a common ancestor over 700 generations ago and are reared in identical habitats. Changes in female fitness resulting from exposure to males from other populations are broadly consistent with sexual coevolution, but, as with most population cross studies, the mechanisms are still poorly understood. To further elucidate the nature and mechanisms of divergence, microarray analysis was performed on the male transcriptomes from a subset of these populations. We report results from this analysis.

24-55 Poster

EXPERIMENTALLY ENFORCED MATINGS IN CALOPTERYX-DAMSELFLIES REVEALS REPEATABILITY IN FEMALE MATING PROPENSITY AND SEXUAL ISOLATION BETWEEN POPULATIONS AND SPECIES

Anna Runemark [1], Erik I. Svensson [1]

[1] *Lund University, Department of Animal Ecology, Ekologihuset, Sölvegatan 37, 223 62, Lund, Sweden*

Anna.Runemark@zooekol.lu.se

We will present experimental data from the field in which we have used a technique of “hand pairing”, in which we enforced females demoiselles (Odonata: *Calopteryx*) to form tandems and/or mate with con- or heterospecfic males. This technique can be used in field studies of odonates to quantify parameters that are otherwise very difficult to estimate in field situations, but which are important in the contexts of speciation processes, in particular to estimate the degree of sexual isolation between populations and species. By presenting female *C. splendens* to male *C. splendens,* either from their own population or from other populations, we were able to quantify the degree of behavioral sexual isolation and female resistance towards mating attempts from immigrant conspecific males. Time from tandem formation to copulation can be used as a measure of female “resistance” or mating propensity. Similarly, by presenting *C. splendens* females to heterospecific males from the same genus (*C. virgo*), we were also able to quantify the degree of behavioural sexual isolation between these two closely related species which are sympatric across large areas in southern Sweden. Finally, by performing “double-pairings” with the same females, we were also able to estimate the repeatability of female resistance and mating propensity, and relate mating speed to the mating order of con- and heterospecific males.

24-56 Poster

COEVOLUTION BETWEEN HARMFUL MALE GENITALIA AND FEMALE RESISTANCE IN SEED BEETLES

Johanna Rönn [1], Göran Arnqvist [1], Mari Katvala [1]

[1] *Uppsala University, Animal Ecology, Norbyvägen 18 d, 75334, Uppsala, Sweden*

Johanna.Ronn@ebc.uu.se

Reproductive conflict between the sexes is thought to be a key force in the evolution of many reproductive characters, but persuasive evidence for its significance is still scarce. The spectacular evolution of male genitalia that impose physical injury on females during mating has often been suggested to be a product of sexually antagonistic coevolution, but our understanding of these extraordinary adaptations is very limited and there is no direct data addressing their evolutionary elaboration. We show that more spiny male genitalia causes more harm to females during copulation and we provide comparative evidence for the correlated evolution between these antagonistic adaptations in males and a female counter adaptation (the amount of connective tissue in the copulatory duct) in a group of insects. By combining comparative and experimental methods, we demonstrate that imbalance of relative armament of the sexes affects evolution of the economics of reproduction: as males evolve genitalia that are more harmful relative to the level of female counter adaptation, costs associated with mating for females increase and population fitness is depressed. Our results unveil a coevolutionary arms race between the sexes and are consistent with a proposed link between sexual conflict, species’ viability and the risk of extinction.

24-57 Poster

MATING SUCCESS AND DEVELOPMENTAL STABILITY OF TWO MALE SEXUAL TRAITS IN DROSOPHILA SUBOBSCURA

Marija Savic [1], Tatjana Savic [2], Sofija Pavkovic - Lucic [1], Marina Stamenkovic - Radak [1], Marko Andjelkovic [1]

[1] *Faculty of Biology, Studentski trg 3, 11000, Belgrade, Serbia*
[2] *Institute for Biological Research, Bulevar despota Stefana 142, 11000, Belgrade, Serbia*

marijas13@yahoo.com

Fluctuating asymmetry (FA) has been used as a measure for developmental stability in numerous studies, giving contradictory results and causing many debates. It has been suggested that fluctuating asymmetry (FA) in secondary sexual traits may be a useful indicator of individual quality in mating choice. We tested this concept using *Drosophila subobscura* under conditions of competitive and non□competitive mating, and compared mating success and fluctuating asymmetry in terms of the number of sex combs and wing size of males. The results will reveal whether female preferences for different sexual traits are influenced by FA under different mating conditions in *Drosophila subobscura*. Because of the role of the wings in male courtship, and sex combs as a secondary sexual trait, it can be persumed that more symmetrical males for this traits would be more successfull in mating. The assocation between individual FA and its ability to minimize various stress effects makes FA an ideal "phenotypic attractant" for discriminating females.

24-58 Poster

EVIDENCE OF MUTUAL SEXUAL SELECTION ON A HOMOLOGOUS ORNAMENT IN THE MOSQUITO SABETHES CYANEUS

Sandra H. South [1]

[1] *EBC, Uppsala University, Dept Animal Ecology, Norbyv 18D, SE-752 36, Uppsala, Sweden*

sandra.south@ebc.uu.se

There are abundant studies of sexually selected male ornaments in polygynous species. In comparison, studies of homologous ornaments expressed in both sexes are scant. I investigated the ornaments of the mosquito *Sabethes cyaneus*, a monandrous species in which both sexes possess striking paddle-like ornaments on their mid-legs. I used geometric morphometrics to explore ornament variation and allometry. A negative correlation between fluctuating asymmetry and body size was found. Paddle shape differed between the sexes. Paddle area increased more rapidly with body size in females than in males, possibly reflecting stronger selection on paddles in females. These data suggest that this may be a monandrous system with mutual mate choice. Thus, *S. cyaneus* provides a unique opportunity to study the evolution of homologous ornaments in a species with a conventional sex role.

24-59 Poster

THE BEHAVIOURAL GENETICS OF SPECIATION IN CICHLID FISHES FROM THE AFRICAN GREAT LAKES

Ola Svensson [1], Katie Woodhouse [1], Ole Seehausen [2, 3], George F. Turner [1]

[1] *University of Hull, Department of Biological Sciences, University of Hull, HU67RX, Hull, United Kingdom*
[2] *EAWAG, Fish Ecology & Evolution, Seestrasse 79, CH - 6047, Kastanienbaum, Switzerland*
[3] *University of Berne, Aquatic Ecology & Macroevolution, Baltzerstrasse 6, CH - 3012, Berne, Switzerland*

o.svensson@hull.ac.uk

There are hundreds of cichlid fish species unique to Lakes Malawi and Victoria in Africa. Many closely-related species can be crossed in the laboratory, but mate assortatively in nature, suggesting that speciation may often be influenced by mate choice behaviour. We are screening inter-species crosses of mouthbrooding cichlids for major genes responsible for male courtship traits and female mate preference. We focus on prezygotic isolation by direct mate preferences. The programme involves crossing selected pairs of species and rearing F_2 hybrids (2^{nd} hybrid generation) to adulthood, then quantifying male courtship traits and female preferences. Results will be presented from a study where eighty F_2 females have been repeatedly given a choice between four males of each of the two parental species (*Pundamilia nyererei* and *P. pundamilia* from Python Island, Lake Victoria) where paternities have been assigned using microsatellite DNA. The males of the two species differ in male nuptial colour (red and blue respectively). Many females have shown consistent preferences for mating with males of one species, suggesting a strongly heritable preference. The results suggest that this preference may be based on a few genes, but probably more than one.

24-60 Poster

HOW DOES THE DIFFERENCE IN SEXUAL CONFLICT OF IN- AND OUTBREEDING PARENTS INFLUENCE OFFSPRING PERFORMANCE?

Timo Thuenken [1], Theo C. M. Bakker [1], Sebastian A. Baldauf [1], Harald Kullmann [1]

[1] *Bonn, Institute for Evolutionary Biology, An der Immenburg 1, 53121, Bonn, Germany*

tthuenken@evolution.uni-bonn.de

Theory predicts that under certain conditions the advantages of inbreeding can override its costs. In social species, it is assumed that the social environment can buffer against inbreeding depression. Here, we investigate the impact of parental care on in- and outbred offspring in *Pelvicachromis taeniatus*, a small cave-breeding cichlid of Western Africa with bi-parental brood care. Previous research has shown that both sexes of the cichlid *P. taeniatus* actively prefer kin as mating partners and that related breeding pairs were more cooperative than unrelated pairs, suggesting a reduced sexual conflict in inbreeding pairs. Inbred offspring revealed no inbreeding depression. However, it was unclear whether this lack of inbreeding depression was due to absence of genetic load or to compensation through high quality parental care. To elucidate this question we compared the survival rate of in- and outbred offspring with and without parental care. We found a significant interaction between parental care and breeding design. Inbred offspring seem to have advantages in the presence of parental care whereas outbred offspring performed better unattended. This result suggests that the degree of relatedness between parents has an important influence on the quality of parental care and thus indirectly on offspring performance and should therefore be incorporated when considering the consequences of in- and outbreeding.

24-61 Poster

CONFLICT AND COOPERATION IN PENDULINE TITS

René E. Van Dijk [1], Jan Komdeur [2], Tamás Székely [1]

[1] *University of Bath, Biology and Biochemistry, Claverton Down, BA2 7AY, Bath, United Kingdom*
[2] *University of Groningen, Animal Ecology Group, Biological Centre, Kerklaan 30, 9750 AA, Haren, The Netherlands*

R.E.van.Dijk@bath.ac.uk

What is the impact of sexual conflict on behaviour of Penduline Tits? The concept of sexual conflict is based on the different evolutionary interests of males and females over reproduction. As such, it has been shown to be a powerful force behind the evolution of behaviour and body size, and it may even facilitate speciation processes. One of our study species, the Eurasian Penduline Tit, exhibits an intense sexual conflict over parental care, whereas in the other, the Cape Penduline Tit, the male and female cooperate in raising the offspring. Firstly, we focus on the Eurasian Penduline Tit. Our detailed observations describe the process of how parents may interact during nest building just before one or both parents desert(s) the clutch. Secondly, we compare this nest building behaviour with that of the socially monogamous Cape Penduline Tit. We argue that it is in the best interest of both Eurasian Penduline Tit parents to disguise their intention to desert. Furthermore, following predictions from sexual conflict theory, we show that the levels of cooperation in the context of the two radically different breeding systems seem to reflect the levels of cooperation in nest building behaviour.

24-62 Poster

VARIATION IN DEWLAP SIZE AMONG POPULATIONS OF THE BROWN ANOLE, ANOLIS SAGREI: A TRADE-OFF BETWEEN NATURAL AND SEXUAL SELECTION?

Bieke Vanhooydonck [1], Anthony Herrel [1], Jay Meyers [2], Duncan J. Irschick [2]

[1] *University of Antwerp, Biology, Universiteitsplein 1, B-2610, Wilrijk, Belgium*
[2] *University of Massachusetts, Biology, 221 Morrill Science Center, MA01003, Amherst, U.S.A.*

bieke.vanhooydonck@ua.ac.be

Anolis lizards are characterized by the possession of an extendable throat fan or dewlap. Dewlap size, shape and colour vary greatly among and within species. In most anoles, both sexes possess a dewlap although males typically have much larger dewlaps than females. In a male-male context, dewlap extensions are believed to represent a “threat” or “challenge” to potential intruders, whereas females appear to choose males based on dewlap characteristics. Also, the dewlap acts as a pursuit-deterrent signal in a predator-prey context. Still, how and under which, potentially opposing, selective pressures dewlap size evolves remains largely unexplored.

Here, we question to which degree sexual selection, natural selection or a combination of both shape the evolution of dewlap size in *Anolis* lizards. To do so, we quantify the variation in dewlap size in the brown anole, *A. sagrei,* from the Bahamas. Seven populations, from seven different islands, were sampled. These islands vary greatly in size (from 0.019 km^2 to 5957 km^2), habitat diversity, number of congeneric species, and predator species and are thus likely to differ in selective regimes. Results from multiple regression analyses show that dewlap size is determined by different ecological factors in males and females. Whereas in males the variation in dewlap size is explained by the variation in island size, tail break frequency (used here as an index of predation pressure), and number of congeneric species, the variation in dewlap size in females is solely explained by the variation in body size. Thus, our data suggest that different selective pressures act on male and female dewlap size in *A. sagrei.*

24-63 Poster

SEXUAL ORNAMENTS AS INDICATORS OF GENETIC QUALITY: OLDER MALES SIGNAL MORE RELIABLY IN ALPINE WHITEFISH

Claus Wedekind [1], Davnah Urbach [1], Alain Jacob [1], Rudolf Müller [2]

[1] *University of Lausanne, Department of Ecology and Evolution, Biophore, 1015, Lausanne, Switzerland*
[2] *Eawag, Swiss Federal Institute of Aquatic Science and Technology, 6047, Kastanienbaum, Switzerland*

Claus.Wedekind@unil.ch

The handicap principle predicts that only high quality individuals can afford costly sexual signals. This original idea was based on the typical life history of semelparous species. Recent theoretical analyses concluded that sexual signals can be quality indicators in species with multiple reproductive bouts, too, but that signal reliability then varies with signalers' age: older males are predicted to signal more reliably. We tested this prediction in the whitefish Coregonus zugensis, a species where males only contribute genes to their offspring. We caught a random sample of 173 breeders from their spawning place, collected their gametes, and used them for in vitro fertilization in 11 full-factorial breeding blocks (North-Carolina II design) in order to disentangle additive genetic variation from non-additive genetic variation and maternal environmental effects on offspring viability. We determined embryo survival under various conditions and found that the average size of the breeding tubercles of 4- and 5-year old males was significantly linked to embryo viability. No such correlation could be found in 3-year old males. Instead, average tubercles size of the younger males was positively linked to their investment into gonads. This suggests that young and old males differ in their signaling strategies, and that breeding tubercles are useful indicators of genetic quality only in older males.

24-64 Poster

GENETIC ARCHITECTURE OF A FEMALE SEXUAL ORNAMENT

Dominic Wright [1], Tommaso Pizzari [2], Leif Andersson [1]

[1] *Uppsala University, IMBIM, Uppsala, Sweden*
[2] *Oxford University, Edward Grey Institute, U.K.*

domwright@gmail.com

Understanding the evolution of sexual ornaments is an enduring challenge in evolutionary biology, and the function of female sexual ornaments is particularly puzzling. Key to this challenge is establishing the relationship between ornament expression and female reproductive investment, and the genetic basis underpinning such relationship. Advances in genomics provide unprecedented opportunities to study the genetic architecture of sexual ornaments in model species. Here, we present a quantitative trait locus (QTL) analysis of a female sexual ornament, the comb of fowl, Gallus gallus, using a large-scale inter-cross between red junglefowl and a domestic line, selected for egg production. First, we demonstrate that female somatic investment in comb reflects female reproductive investment. Despite a trade-off between reproductive and skeletal investment mediated by the mobilisation of skeletal minerals for egg production, females with proportionally large combs also had relatively high skeletal investment. Second, we identify a major QTL for bi-sexual expression of comb mass and several QTL specific to female comb mass. Importantly, QTL for comb mass were clustered with QTL for female reproductive and skeletal investment on chromosomes one and three. Together, these results shed light onto the physiological and genetic architecture of a female ornament.

24-65 Poster

EXPERIMENTALLY DISTINGUISHING THE EFFECTS OF FAMILIARITY, RELATEDNESS, PATTERN RARITY AND ORNAMENTATION ON MATE CHOICE IN GUPPIES

Susanne Zajitschek [1], Robert Brooks [1]

[1] *University of NSW, School of Biological, Earth and Environmental Sciences, Australia*

susanne.zajitschek@student.unsw.edu.au

Mate choice has been shown in various species to depend on the magnitude of multiple signal traits as well as context-dependent cues such as familiarity and relatedness between potential mates and rarity of male phenotype. The effects of these factors are often obscured by the fact that they can be correlated with one another. Here, we experimentally disentangle these effects on female mate choice in the guppy (*Poecilia reticulata*). We show that the rarity of the colour pattern is the most important context-dependent factor influencing female mating decisions, with common patterns being most unattractive. Neither visual familiarity nor relatedness between mating partners had any significant effect. Ornamental colour traits significantly influenced female mating decisions independent of the context-dependent measures. Our approach highlights the complexity of female mate choice decisions and the value of combining multifactorial experiments with multivariate selection analyses.

24-66 Poster

FEMALE FOREHEAD PATCH SIZE INDICATES "QUALITY" AND PREDICTS PAIRING STATUS IN COLLARED FLYCATCHERS (FICEDULA ALBICOLLIS)

Markus Zöttl [1], Chris Wiley [1], Nina Svedin [1], Anna Qvarnström [1]

[1] *University Uppsala, Animal Ecology, Norbyvägen 18D, 75236, Uppsala, Sverige*

mazo.3993@student.uu.se

The evolution, function and maintenance of male secondary sexual traits are well understood. However, little attention has been paid to sexually selected traits in the most choosy sex (often females) and female ornamentation is often assumed to be a non-adaptive by-product of selection for ornamentation in males. A recent debate challenges this view on female ornamentation, since some evidence suggests that females may also advertise their qualities as predicted by sexual selection theory. The forehead patch is a sexually selected trait in male collared flycatchers. However, female flycatchers also possess reduced versions of the trait. Here we show that the size of a female's forehead patch increases with age (as in males) and that the size of the trait is positively correlated with body condition and survival probability. Moreover, females with bigger patches were better able to avoid pairing with polygynous males (associated with significant fitness costs). We discuss the possibility that female patch size functions as a signal under sexual selection. We also discuss how expression of the forehead patch in both sexes influences its evolution.

Evolution of unusual gene organisation: an exception or rule?

25

Tuesday August 21 *Location*: Ekonomikum 1

Symposium 25: Evolution of unusual gene organisation: an exception or rule?

ORGANIZERS: Kateryna Makova, Penn State University, USA
Anton Nekrutenko, Penn State University, USA

09.45-10.15	**Wen-Hsiung Li** (invited) Overlapping genes in the human, chimpanzee, and mouse genomes
10.15-10.45	**Laurent Duret** (invited) The origin of an RNA gene: since when does Xist eXist?
10.45-11.05	**Hans Ellegren** Faced with inequality: Chicken does not have a general dosage compensation of sex-linked genes
11.05-11.35	*Coffee*
11.35-11.55	**Francisco Ubeda de Torres** Family matters: evolution of genomic imprinting with bi-parental care
11.55-12.15	**Emmanuelle Porcher** Evidence of large heritable variation for quantitative traits following genome-wide alterations of DNA methylation in Arabidopsis thaliana.
12.15-12.35	**Deniz Dali** Sense-antisense gene pairs: conservation of expression patterns
12.35-14.00	*Lunch*
14.00-14.20	**Julien Roux** Bias in retention of duplicate genes from a whole-genome duplication gives insights into evolution of development in vertebrates
14.20-14.40	**Andrew Heidel** Mitochondrial genome evolution in the social amoebae
14.40-15.00	**Olga Novikova** Distribution and evolution of non-LTR retrotransposons in fungi
15.00-15.20	**Philippe Gayral** Integrations of banana streak virus sequences in the genome of the banana Musa balbisiana - Endogenous viruses or host genes?
15.20-16.00	*Coffee*

25-01 Talk

OVERLAPPING GENES IN THE HUMAN, CHIMPANZEE, AND MOUSE GENOMES

Wen-Hsiung Li [1], Chaitanya Sanna [2], Liqing Zhang [2]

[1] *University of Chicago, Department of Ecology and Evolution, USA*
[2] *Virginia Tech, Computer Science, USA*

whli@uchicago.edu

Increasing evidence suggests that overlapping genes are common in eukaryotic genomes. In this study we identified the overlapping genes in a set of 13484 orthologous genes in the genomes of human, chimpanzee, and mouse, and contrasted the patterns of overlapping between two types of overlapping genes: same-strand overlaps and different-strand overlaps. About 10% of the genes in the orthologous gene set are overlapping genes and the majority of them belong to different-strand overlaps. The three species studied show very similar overlapping patterns. In particular, the majority of the same-strand overlaps are embedded forms whereas the majority of different-strand overlaps are in convergent orientation of gene expression. The majority of overlapping regions are limited to noncoding regions. For same-strand overlaps, most of the overlapping gene pairs show at least a tenfold difference in gene length, a pattern not found in non-overlapping neighboring gene pairs in the genomes. In contrast, for different-strand overlaps, the length difference between the two overlapping genes is less dramatic and is more similar to that of non-overlapping neighboring genes. Different-strand-overlapping relationships are more evolutionarily conserved than are same-strand-overlapping relationships, probably due to the fact that overlaps on different strands are associated with coupled sense and antisense genes. Finally, we show that 3-UTR evolution plays an important role in the transitions between non-overlapping genes and overlapping genes.

25-02 Talk

THE ORIGIN OF AN RNA GENE: SINCE WHEN DOES XIST EXIST ?

Laurent Duret [1], Corinne Chureau [2], Sylvie Samain [3], Jean Weissenbach [3], Philip Avner [2]

[1] *CNRS, Université de Lyon, Biométrie et Biologie Evolutive, 69622, Villeurbanne, France*
[2] *Institut Pasteur, Paris, France*
[3] *Genoscope, Evry, France*

duret@biomserv.univ-lyon1.fr

The Xist noncoding RNA is the key initiator of the process of X chromosome inactivation in eutherian mammals, but its precise function and origin remain unknown. Although Xist is well conserved among eutherians, until now, no homolog has been identified in other mammals. We show here that Xist evolved, at least partly, from a protein-coding gene and that the loss of protein-coding function of the proto-Xist coincides with the four flanking protein genes becoming pseudogenes. This event occurred after the divergence between eutherians and marsupials, which suggests that mechanisms of dosage compensation have evolved independently in both lineages.

25-03 Talk

FACED WITH INEQUALITY: CHICKEN DOES NOT HAVE A GENERAL DOSAGE COMPENSATION OF SEX-LINKED GENES

Hans Ellegren [1]

[1] *Uppsala University, Dept of Evolutionary Biology, Norbyvägen 18D, SE-752 36, Uppsala, Sweden*

Hans.Ellegren@ebc.uu.se

The contrasting dose of sex chromosomes in males and females potentially introduces a large-scale imbalance in levels of gene expression between sexes, and between sex chromosomes and autosomes. In many organisms dosage compensation by epigenetic modification has thus evolved to equalize sex-linked gene expression in males and females. In mammals this is achieved by X chromosome inactivation and in flies and worms by up- or down-regulation of X-linked expression, respectively. While otherwise widespread in systems with heteromorphic sex chromosomes, the case of dosage compensation in birds (males ZZ, females ZW) remains an unsolved enigma. We have used a microarray approach to show that chicken embryos generally express higher levels of Z-linked genes than female birds, both in soma and in gonads. The distribution of male-to-female fold-change values for Z chromosome genes is wide and has a mean of 1.4-1.6, which is consistent with absence of dosage compensation and sex-specific feedback regulation of gene expression at individual loci. Intriguingly, without global dosage compensation, female chicken has significantly lower expression levels of Z-linked compared to autosomal genes, which is not the case in male birds. The pronounced sex difference in gene expression is likely to contribute to sexual dimorphism among birds, and potentially has implication to avian sex determination. This demonstrates the first example of an organism with a lack global dosage compensation, providing an unexpected case of a viable system with large-scale imbalance in gene expression between sexes.

25-04 Talk

FAMILY MATTERS: EVOLUTION OF GENOMIC IMPRINTING WITH BI-PARENTAL CARE

Francisco Ubeda de Torres [1]

[1] *Oxford University, St John's College, St John's College, OX1 3JP, Oxford, UK*

francisco.ubeda@sjc.ox.ac.uk

The Kinship Theory of the Evolution of Genomic Imprinting assumes that all offspring resources come from their mother. However paternal care has been well documented in nine per cent of mammalian genera including taxa such as rodents, carnivores and primates. In this research I remove such restrictive assumption and extend the Kinship Theory to consider the evolution of Genomic Imprinting when both parents contribute offspring resources.

I start by developing a model that allows for any combination of maternal and paternal contribution of resources. This model may account for changes in such combination that may happen after birth or lactation. Then I identify sources of conflict between maternally and paternally inherited genes given that a certain amount of resources has been contributed by each parent. Finally, I use this model to analyse the peculiar phenotype of Prader-Willi and Angelman syndrome.

Prader-Willi syndrome is caused by the lack of expression of paternally inherited genes in region q11-13 of human chromosome 15. Children suffering from Prader-Willi syndrome exhibit a complex clinical phenotype with poor suckling before weaning but a voracious appetite afterwards. I argue that a change in the rate of maternal and paternal contribution happening after lactation may explain the biphasic clinical phenotype shown by Prader-Willi syndrome patients and the lack of it in Angelman syndrome patients.

25-05 Talk

EVIDENCE OF LARGE HERITABLE VARIATION FOR QUANTITATIVE TRAITS FOLLOWING GENOME-WIDE ALTERATIONS OF DNA METHYLATION IN ARABIDOPSIS THALIANA

Emmanuelle Porcher [1, 2], Frank Johannes [2], Vera Saliba-Colombani [2], Matthieu Simon [2], Nicolas Agier [3], David Bouchez [2], Christine Dillmann [4], Philippe Guerche [2], Frédéric Hospital [2], Vincent Colot [3]

[1] *Muséum national d'Histoire naturelle, UMR 5173 CERSP, 61 rue buffon, 75005, Paris, France*
[2] *INRA, Station de Génétique et d'Amélioration des Plantes, 78026, Versailles cedex, France*
[3] *INRA/CNRS/UEVE, Unité de Recherche en Génomique Végétale, 91057, EVRY cedex, France*
[4] *Univ. Paris XI/INRA, Station de Génétique Végétale, 91190, Gif-sur-Yvette, France*

porcher@mnhn.fr

So far, the study of heritable variation of phenotypic traits has mostly focused on DNA sequence polymorphism. However, we now know that the nucleotide sequence is not the only form of genetic information in eukaryotic cells: DNA methylation can also be inherited, both mitotically and meiotically, with important phenotypic consequences (“epimutations”). Such a source of heritable phenotypic variation could help geneticists bridge the long lasting gap between two apparently contradictory observations: the high degree of DNA polymorphism observed in natural populations and the continuous action of natural selection, which should erode this variability.

We have taken an experimental approach with the model plant species *Arabidopsis thaliana* to study the ability of epimutations to generate a potentially adaptive genetic variation independently of any DNA polymorphism. Using two parental lines with virtually identical DNA sequence, but differing by their methylation pattern, we built 500 recombinant inbred lines (epiRILs). These epiRILs were evaluated at generation BC1-S7 for several traits related to fitness in order to quantify the level of phenotypic variation possibly induced by epimutations. We show that phenotypic variation among epiRILs is orders of magnitude larger than that observed in mutation accumulation experiments, and must have arisen as a direct or indirect consequence of alterations in DNA methylation.

25-06 Talk

SENSE-ANTISENSE GENE PAIRS: CONSERVATION OF EXPRESSION PATTERNS

Deniz Dali [1], Martin J. Lercher [1]

[1] *Heinrich-Heine-University Düsseldorf, Bioinformatics, Universitätsstr. 1, D-40225, Düsseldorf, Germany*

lercher@cs.uni-duesseldorf.de

While up to 20% of mammalian genes form sense-antisense pairs, the regulatory mechanism and significance of these pairs is still debated. It has been suggested that this form of genomic organisation allows precise co- or anti-regulation of the two genes. Such regulatory roles would not only result in correlated or anti-correlated expression in a single species, but importantly also in conservation of the mode of expression across species. Here, we report the results of a comparison of whole-genome expression data of coding and non-coding genes across mammalian species.

25-07 Talk

BIAS IN RETENTION OF DUPLICATE GENES FROM A WHOLE-GENOME DUPLICATION GIVES INSIGHTS INTO EVOLUTION OF DEVELOPMENT IN VERTEBRATES

Julien Roux [1], Marc Robinson-Rechavi [1]

[1] *University of Lausanne / Swiss Institute of Bioinformatics, Department of Ecology and Evolution, Biophore - UNIL Dorigny, 1015, Lausanne, Switzerland*

julien.roux@unil.ch

Teleost fishes have experienced an ancient whole genome duplication. More than 80% of the duplicate genes have been rapidly lost, and importantly the retained duplicates represent a subset biased by selective pressures. Here, we use this biased retention as a measure of selective pressures during development.

Combining transcriptome data and phylogeny, we show that genes expressed in early development are counter-selected for retention of duplicates, and that this trend is conserved between species. These results suggest that early stages of vertebrate development are less open to innovations from genome duplication than late stages.

This can be explained by an underlying progressive decrease of genetic constraints in development, and we suggest a "von Baer-like" model at the genetic level. This does not contradict the "hourglass" model used for morphology, but describes a different level of organization. Our transcriptome-focused point of view can be a good way of linking molecular and morphological data, i.e. genotype and phenotype.

25-08 Talk

MITOCHONDRIAL GENOME EVOLUTION IN THE SOCIAL AMOEBAE

Andrew J. Heidel [1], Gernot Glöckner [1]

[1] *Fritz-Lipmann Institute, Genome Analysis, Beutenbergstr. 11, 07745, Jena, Germany*

aheidel@fli-leibniz.de

A whole genome sample sequencing project in the social amoebae group provided us with a set of complete mitochondrial genomes from Dictyostelium citrinum, Polysphondylium pallidum and D. fasciculatum. These genomes plus the previously sequenced model species D. discoideum and the related solitary amoeba, Acanthamoeba castellanii, within this deeply branching phylogenic group allow comparative genomic studies of the mitochondrial genomes. Mitochondrial genomes differ greatly in size and gene content across eukaryotes, however the social amoebae and A. castellanii have largely similar gene content enabling a number of molecular evolutionary studies. The gain or loss of genes can identify if any genes have been exchanged between the mitochondrial genome and the nuclear genome. Comparisons of individual gene phylogenies can identify if any genes have different evolutionary paths or whether they follow the organismal phylogeny. We also tested the effects of a segmental rearrangement in D. discoideum and D. citrinum on evolutionary rates in individual genes. Finally the genetic code in the social amoebae is the universal code while nearby relatives such as A. castellanii have alternative codes permitting tests of the effect of the different codes on codon usage and gene evolution.

25-09 Talk

DISTRIBUTION AND EVOLUTION OF NON-LTR RETROTRANSPOSONS IN FUNGI.

Olga Novikova [1]

[1] *Institute of Cytology and Genetics SIB RAS, Molecular Evolution, pr. Lavrentyeva 10, 630090, Novosibirsk, Russia*

novikova@bionet.nsc.ru

Retrotransposons are mobile genetic elements that propagate themselves by reverse transcription of an RNA intermediate. There are two major classes of retrotransposons, which differ structurally and mechanistically: LTR retrotransposons present long terminal repeats (LTRs) and have a transposition mechanism similar to that of retroviruses, whereas non-long terminal repeat (non-LTR) retrotransposable elements do not carry terminal repeats and employ a simpler target-primed reverse transcription (TPRT) mechanism for retrotransposition. Transposition of non-LTR elements causes hybrid disgenesis in Drosophila and genetic diseases in human, and has been implicated in the emergence of pseudogenes and exon shuffling. In this context non-LTR retrotransposons play important roles in the structural organization and evolution of the genomes in which they are found.

Fungi have small genomes, which, as a rule, contain only limited amounts of repetitive DNA. Among the Eumycota, the evolutionary younger divisions, Ascomycota and Basidiomycota, have a strong tendency towards streamlined genomes. Representatives of Eumycota contains not more than 10-15 % repetitive DNA, including retrotransposons.

More than sixty fungal species are available in public databases today belonged to main fungal groups – Microsporidia, Zygomycota, Chytridiomycota, Ascomycota, and Basidiomycota. We implemented in silico analysis of their whole genomic sequences and isolated new non-LTR retroelements from 34 species. Majority of investigated fungi gave us positive results during the in silico search of non-LTR retrotransposons. The newly described non-LTR retrotransposons were systematized.

25-10 Talk

INTEGRATIONS OF BANANA STREAK VIRUS SEQUENCES IN THE GENOME OF THE BANANA MUSA BALBISIANA - ENDOGENOUS VIRUSES OR HOST GENES?

Philippe Gayral [1], Nathalie Laboureau [1], Marie-Line Iskra-Caruana [1]

[1] *UMR BGPI, CIRAD BIOS, Campus Intal Baillarguet TA-A54/K, 34398, Montpellier, France*

philippe.gayral@cirad.fr

Banana streak virus or BSV (*Badnavirus*) is a double stranded DNA pararetrovirus causing leaf streak mosaic disease. Recently, numerous outbreaks of the disease occurred in all banana producing areas in interspecific *Musa* hybrids (*M. acuminata* x *M. balbisiana*) originating from virus-free parents. These infections correlated with BSV DNA sequences integrated in the *M. balbisiana* genome only, called endogenous pararetroviruses (EPRVs). Although integration is not needed for the replication cycle, some BSV EPRVs could become infectious under stress conditions by reconstituting a replication-competent genome after homologous recombination events. Surprisingly, even though the wild *M. balbisiana* Pisang Klutug Wulung (PKW) harbours pathogenic BSV EPRV, it is resistant to the virus. In these conditions, how to explain such viral integrants fixed in the host genome in terms of cost and benefits for both plant and virus? In order to highlight this question, we retraced the evolutionary history of infectious EPRVs of Golfinger species (BSGfV) integrated at a single locus in the genome of PKW. The structure of this EPRV was characterized in PKW by sequencing BAC clones containing BSGfV EPRVs. The integrant is composed of back-to-back viral sequences representing more than a whole genome. We developed molecular markers to explore the polymorphism of BSGfV integration patterns among *M. balbisiana* genotypes and other *Musa* species representing the genetic diversity of the genus. BSGfV EPRVs showed the same integration pattern as PKW in all *M. balbisiana* and a modified pattern in the relative species *M. boman*. Any BSGfV EPRV was observed in the other *Musa* species. We assume that BSGfV integrated its host recently. Phylogenetic analysis combining sequence data from both virus and EPRV confirmed this result. The consequences for *Musa* harbouring potentially deleterious sequences which have rapidly been fixed will be discussed.

25-01 Poster

THE ORIGIN OF ALPHA-AMYLASES IN METAZOA

Jean-Luc Da Lage [1], Etienne G. J. Danchin [2], Didier Casane [1]

[1] *CNRS, LEGS, Avenue de la Terrasse, 91198, Gif sur Yvette, France*
[2] *CNRS, AFMB-UMR 6098, Case 932, 163 Avenue de Luminy, 13288, Marseille cedex 09, France*

jldl@legs.cnrs-gif.fr

Alpha-amylases are widely found in Eukaryotes and Prokaryotes. Few amino acids are conserved among these organisms, but at an intra-kingdom level, conserved protein domains exist. In animals, numerous conserved stretches are considered as typical of animal α-amylases. Searching databases, we found no animal-type α-amylases outside the Bilateria. Instead, we found in the sponge Reniera sp. and in the sea anemone Nematostella vectensis, α-amylases whose most similar cognate was that of the amoeba Dictyostelium discoideum. We found that this "Dictyo-type" α-amylase was shared not only by these non-Bilaterian animals, but also by other Amoebozoa, Choanoflagellates, and Fungi. This suggested that the Dictyo-type α-amylase was present not only in the last common ancestor of Unikonts but also in the first Metazoa. The additional presence of the Dictyo-type in some Ciliates and Excavates, suggests that horizontal gene transfers may have occurred among Eukaryotes. We have also detected putative interkingdom transfers of amylase genes, which obscured the historical reconstitution. Obviously, several scenarii are possible, but one is favored: the animal-type amylase would have originated in a small group of Proteobacteria (Alteromonadaceae) and would have been then transferred to the ancestor of Bilateria, and also to a few other unrelated Bacteria.

25-02 Poster

EVOLUTIONARY ASPECTS OF THE CONTROVERSIAL H2ABBD (BARR BODY DEFICIENT) HISTONE VARIANT

Jose M. Eirin-Lopez [1, 2], Toyotaka Ishibashi [1], Juan Ausio [1]

[1] *University of Victoria, Biochemistry and Microbiology, Petch Building, Room 258, V8W3P6, Victoria, Canada*
[2] *Universidade da Coruna, Biologia Celular Y Molecular, Facultade de Ciencias, Campus de a Zapateira S/N, 15071, A Coruna, Spain*

che@uvic.ca

In the eukaryotic cell nucleus, the packaging of nucleic acids is achieved through their interaction with histone proteins, assembling nucleosome core particles which represent the fundamental units of the chromatin fiber. Histones and their variants are responsible for organizing the chromatin complex and within this context they can be classified into core histones (H2A/H2B, H3/H4) and linker histones (histones of the H1 family). Histone variants are critical to fulfill specific duties in the cell related to chromatin packaging, dynamics and metabolism during different stages of the cell cycle, in different cell types, and developmental stages. Within the H2A histone family, the histone variant H2ABbd (Barr body deficient) represents one of the hottest topics in current chromatin research, given its exclusion from the inactive X chromosome from mammals and its still unveiled role in chromatin structure and dynamics. From an evolutionary point of view, histone H2ABbd is very interesting for being present only in mammalian lineages so far, as well as for the reduced levels of synonymous variation and the more abundant amino acid replacements observed respect to canonical H2A histones, when compared with other histone variants. The present work represents the first approach to the characterization of the evolutionary features displayed by the H2ABbd histone variant, including the evolutionary mechanisms governing its long-term change within the H2A family and their significance in terms of structure and function.

25-03 Poster

COMPARATIVE GENOMIC ANALYSIS OF THE ODORANT BINDING PROTEIN MULTIGENE FAMILY IN DROSOPHILA

Filipe G. Vieira [1], Alejandro Sanchez-Gracia [2, 1], Julio Rozas [1]

[1] *Universitat de Barcelona, Genetica, Av Diagonal, 645, 08028, Barcelona, Spain*
[2] *Instituto Cajal - CSIC, Neurobiología del Desarrollo, 28002, Madrid, Spain*

fgarret@ub.edu

Chemoreception is a widespread mechanism involved in critical biological processes, being essential for the detection of sources of food, egg-laying substrates, mates and predators, and allowing for communication and social coordination. The insect peripheral olfactory-system comprises three major multigene families, the olfactory receptor (OR), the gustatory receptor (GR) and the odorant-binding protein (OBP) families.

We performed a comparative analysis of the OBP family in twelve *Drosophila* genomes. We identifed 643 genes (595 OBPs and 48 CSPs –chemosensroy proteins) encoding putative functional and non-functional members in extant species, inferring 43 gene gains and 28 gene losses (15 deletions and 13 pseudogenization events) in the OBP gene family. The analysis shows that duplicate members mainly arise from tandem gene duplication and progressively diverge in DNA and amino acid sequence and that the pseudogenization events are predominant in the external branches of the phylogenetic tree. We observed that the OBP arrangement in clusters is maintained across the *Drosophila* species, pointing to some functional significance of this organization. Overall, the phylogenetic relationship among orthologous and paralogous OBP members noticeably supports the birth-and-death model for the evolution of this multigene family. Under this model we estimated the birth-and-death rate as 0.002-0.008 per gene and per million years.

25-04 Poster

VERTEBRATE CHROMOSOME DUPLICATIONS AND THE NEUROPEPTIDE Y RECEPTOR PARALOGON

Tomas A. Larsson [1], Frida Olsson [1], Görel Sundström [1], Lars-Gustaf Lundin [1], Sydney Brenner [2], Byrappa Venkatesh [2], Dan Larhammar [1]

[1] *Uppsala University, Neuroscience, BMC Husargatan3, BOX 593, 75124, Uppsala, Sweden*
[2] *A*STAR Biomedical Sciences Institutes, Institute of Molecular and Cell Biology, 61 Biopolis Drive, Singapore*

Tomas.Larsson@neuro.uu.se

Two genome duplications are thought to have occurred before the origin of jawed vertebrates (gnathostomes) and one additional in the actinopterygian fish lineage before the origin of euteleost fish. One of the many gene families that expanded in early vertebrate evolution is the neuropeptide family (NPY) of G-protein coupled receptors. In this study we have constructed phylogenetic trees for several gene families physically located close to the NPY receptor genes in the compact genomes of the teleost fishes Tetraodon nigroviridis and Takifugu rubripes. All ENSEMBL family members from several vertebrates were investigated and at least one invertebrate sequence was included for relative dating of duplication events. Chromosome regions with conserved synteny were identified and confirmed by phylogeny in Homo sapiens, Mus musculus, Danio rerio, Takifugu rubripes and Tetraodon nigroviridis. A total of 25 gene families showed topology consistent with an expansion in vertebrate evolution by supporting either duplications before the radiation of gnathostomes or in the actinopterygian lineage. RT-PCR carried out from several tissues in T. rubripes revealed that all five NPY receptors were expressed in the brain. The three receptor subtypes Y2, Y4 and Y8 were also expressed in several other organs. The NPY receptors Y1 and Y5 which in mammals mediate the appetite-stimulating effect of NPY are absent in all three fully sequenced fish genomes and were probably lost in the teleost ancestor. The phylogenetic analyses of these gene families support duplications of large blocks of genes or even entire chromosomes forming the NPY receptor paralogon, consistent with two early vertebrate tetraploidizations and one teleost tetraploidization.

25-05 Poster

THE STRUCTURE AND EVOLUTION OF THE AUSTRALIAN LUNGFISH GENOME

Cushla J. Metcalfe [1], Joss Jean [2], Didier Casane [1]

[1] *Centre National de la Recherche Scientifique, Laboratoire Evolution, Génomes et Spéciation, 1 Ave de la Terrasse, 91198, Gif-sur-Yvette, France*
[2] *Macquarie University, Department of Biological Sciences, Balaclava Road, 2109, North Ryde, Australia*

cushla.metcalfe@legs.cnrs-gif.fr

Most modern fishes are ray-finned fishes. The Australian lungfish, however, is a lobe-finned fish (a sarcopterygian fish) and it is from the sarcopterygians that the land vertebrates are thought to have arisen during the Devonian, some 350 million years ago. Today there are only 8 extant species of lobe-finned fish, 2 coelacath and 6 lungfish species. The lungfish are generally considered to be more closely related to the land vertebrates and are, therefore, important to our understanding of the transition from water to land. Our lab in Sydney is the only research institute in the world that breeds lungfish, and so it is the Australian lungfish that we are focussing on. Our interest is in the evolutionary developmental and structural aspects of its genome.

The structure of the Australian lungfish genome is additionally interesting because of its size, it has one of the largest vertebrate genomes. Genome size is a unique trait because it lies at the interface between genome and phenotype; genome size affects cell size, cell division rate, developmental and growth rates and metabolic rate (in some groups). We are interested in these phenotypic effects of a large genome in the Australian lungfish, as well as the overall structure of the lungfish genome; for example, CG% structuring, intron size and composition and number, type, time of insertion and possible activity of transposable elements. Eukaryotic genomes have about 10^4 genes, the differences in genome size is due to differences in amounts of non-coding DNA. The larger the genome, the more transposable elements appear to contribute to that this non-coding component, relative to other sources of variation. We therefore suspect that lungfish genome is chiefly composed of transposable elements. Here we will present preliminary work on transposable elements identified and characterised in the Australian lungfish.

25-06 Poster

A FIRST LOOK AT ARFOME: DUAL-CODING GENES IN MAMMALIAN GENOMES

Anton Nekrutenko [1], Wen-Yu Chung [1], Samir Wadhawan [1], Radek Szklarczyk [2]

[1] *Penn State University, Center for Comparative Genomics and Bioinformatics, 505 Wartik Lab, 16802, University Park, PA, USA*
[2] *Vrije Universiteit, Integrative Bioinformatics Institute, Amsterdam, Netherlans*

anton@bx.psu.edu

A textbook human gene encodes a protein using a single reading frame. Alternative splicing brings some variation to that picture, but the notion of a single reading frame remains. Although this is true for most of our genes, there are exceptions. Like viral counterparts, some eukaryotic genes produce structurally unrelated proteins from overlapping reading frames. The examples are spectacular (G-protein alpha subunit [Gnas1] or INK4a tumor suppressor), but scarce. The scarcity is anthropogenic in origin: we simply do not believe that dual-coding genes can occur in eukaryotes. To challenge this assumption, we performed the first genome-wide scan for mammalian genes containing alternative reading frames located out of frame relative to the annotated protein-coding region. Using a newly developed statistical framework, we identified 40 such genes. Because our approach is very conservative, this number is likely a significant underestimate, and future studies will identify more alternative reading frame–containing genes with fascinating biology.

25-07 Poster

STUDIES OF THE GROWTH HORMONE-PROLACTIN GENE FAMILY AND THEIR RECEPTOR FAMILY IN RELATION TO VERTEBRATE TETRAPOLIDIZATIONS

Daniel Ocampo Daza [1], Görel Sundström [1], Tomas A. Larsson [1], Dan Larhammar [1]

[1] *Uppsala University, Neuroscience, BMC, Husargatan 3 Box 593, 751 24, Uppsala, Sweden*

daniel.ocampo.daza@gmail.com

The growth hormone and prolactin genes are part of the same gene family and were formed through a duplication of an ancestral gene in early vertebrate evolution. These genes are represented in all vertebrate groups and the proteins perform many well-studied functions. A third member of the family, somatolactin, is found throughout ray-finned fishes as well as in lungfishes. Two forms of somatolactin have been identified in some teleost fishes supporting duplication of this gene in early teleost evolution, possibly in the teleost tetraploidization (3R). In the species studied the GH and PRL receptor genes, which belong to the large family of class-1-cytokine receptors, are located on the same chromosome suggesting that one arose from the other in a local duplication event. Somatolactin has a separate related receptor that has so far only been identified in two species. Ensembl family sequences from several species representing major vertebrate groups were used to create phylogenetic trees of the GH-PRL family as well as the receptor family. Additional trees were made using sequences from gene families with members in at least two of the selected regions within approx. 5 MB in each direction of the peptide genes in the zebrafish Danio rerio. At least one invertebrate sequence was included in the trees (except in the GH family) to get relative dates for the duplication events. These phylogenetic analyses as well as the chromosome location of the genes in the different species suggest that the origin of the gene family coincides with the proposed early vertebrate whole genome duplication events (2R). We have also addressed the recent proposition that the growth hormone receptor genes identified in most fish species is actually the somatolactin receptor and have performed phylogenetic analyses suggesting that this is indeed the case. To resolve the origin of the somatolactin receptor gene relative to the GH and PRL receptor genes requires additional studies including chromosomal location. In any event, these studies show that the growth hormone-prolactin proteins and their receptors arose in early vertebrate evolution.

25-08 Poster

COMPACT GENES ARE HIGHLY EXPRESSED IN THE MOSS PHYSCOMITRELLA PATENS

Hans K. Stenøien [1]

[1] *Norwegian University of Science and Technology, Department of Biology, Høgskoleringen 5, 7491, Trondheim, Norway*

stenoien@bio.ntnu.no

Compact genes contain short and few introns, and they are highly expressed in different animal genomes. Recently, it has been shown that in *Oryza sativa* and *Arabidopsis thaliana*, highly expressed genes tend to be least compact, containing long and many introns. It has been suggested that selection on genome organization may have acted differently in plants compared to animals. Here it is shown that in the haploid moss *Physcomitrella pates*, highly expressed genes contain shorter introns than genes with low expression levels. This study therefore supports the hypothesis that selection may act strongly favouring transcriptional efficiency at least in the haploid phase of plant life cycles. It is concluded that plants do not necessarily respond to other selection pressures than animals regarding genome structuring.

25-09 Poster

EVOLUTION OF THE HOX PARALOGON IN VERTEBRATES

Görel Sundström [1], Tomas A. Larsson [1], Dan Larhammar [1]

[1] *Uppsala University, Neuroscience, BMC, Box 593, 751 24, Uppsala, Sweden*

gorel.sundstrom@neuro.uu.se

Since the theory about two whole genome duplications (2R) in the vertebrate lineage emerged, the Hox gene clusters (located on human chromosomes 2, 7, 12 and 17) have been used as the prime example of quadruplicate paralogy in vertebrate genomes. At the same time, the Hox clusters are known to be special in many ways, particually in the way they are transcriptionally regulated. In ray-finned fishes, a third tetraploidization (3R) has been inferred based on the existence of additional Hox clusters not present in other vertebrate lineages. This has thereafter been confirmed using whole genome data from fully sequenced teleosts. Since each Hox cluster is located on a rather limited part of the chromosome, studies of syntenic gene families are needed to fully understand the evolutionary history of the Hox chromosomes.

In this work we have made phylogenetic analysis of gene families located near the Hox clusters in several vertebrates in order to see if there are additional gene families with an evolutionary history similar to that of the Hox clusters. Our starting point was the genes for the NPY family peptides in the pufferfish *Takifugu rubripes* and the zebrafish *Danio rerio*, compared to the positions in the human genome. We have analyzed 14 gene families using both neighbour joining and maximum likelihood methods. All of the families had a topology that supports origin by chromosomal duplications (by extension supporting 2R), and all but two are also compatible with the teleost-specific duplication.

Based on this analysis we can conclude that not only the Hox clusters evolved by block or chromosome duplication in early vertebrates, several other gene families also seem to have expanded by the same mechanism, presumably providing raw material for the emergence of new functions or more specialized functions, i.e., neofuntionalization and subfunctionalization.

25-10 Poster

THE EARLY EVOLUTION OF THE OPIOID RECEPTOR FAMILY IN VERTEBRATES

Görel Sundström [1], Susanne Dreborg [1], Tomas A. Larsson [1], Dan Larhammar [1]

[1] *Uppsala University, Neuroscience, BMC, Box 593, 751 24, Uppsala, Sweden*

gorel.sundstrom@neuro.uu.se

Four opioid receptors are present in mammals, called delta, kappa, mu and orphanin receptor, forming a family of receptors that arose from a common ancestor. We have investigated the evolution of the opioid receptors in vertebrates by using phylogenetic studies in combination with chromosomal location of the genes in several species representing major vertebrate groups. We used the Ensembl database and studied genes within approximately 14 MB around each opioid receptor gene, and then phylogenetically analyzed all gene families with members in at least two of the selected regions. In total, we analyzed 21 gene families where we, besides human sequences, also used sequences from dog, chicken, the frog X*enopus tropicalis*, green spotted pufferfish (*Tetraodon nigroviridis*) and either *Ciona intestinalis* or *Ciona savignyi*. The gene family trees (except the opioid receptor family) were rooted with sequences from the fruit fly, *Drosophila melanogaster*. Fifteen of these families displayed a topology supporting origin by duplication during early vertebrate evolution.

It seems like the receptor genes are located in a paralogon with members on human chromosomes 1, 6, 8 and 20 and that most likely this quartet of chromosome regions was formed concomitantly with, and thus resulting from, the two early vertebrate whole genome duplications. There are also some indications that the opioid peptides may have evolved in a similar way – by chromosome duplications, but due to major rearrangements in the mammalians, the picture is still unclear. Thus, the system of opioid peptides and receptors reached it present complexity already more than 450 Myr ago, at the dawn of gnathostome evolution.

Ageing and senescence in wild animal populations

26

Friday August 24 *Location*: Ekonomikum 1

Symposium 26: Ageing and senescence in wild animal populations

ORGANIZERS: Anne Charmantier, CNRS, Montpellier, France
Dan Nussey, University of Cambridge, UK

9.45-10.15	**James Carey** (invited) Population aging and extraordinary life span in wild medflies
10.15-10.45	**Anne Bronikowski** (invited) Physiological evolution and rate of aging in wild populations of the garter snake (Thamnophis elegans)
10.45-11.05	**Thomas Reed** Reproductive senescence in a long-lived species: rates of decline in late life performance are associated with varying costs of early reproduction
11.05-11.35	*Coffee*
11.35-11.55	**Petteri Ilmonen** Telomere attrition due to chronic infection
11.55-12.15	**Paul Schmidt** Reproductive diapause and aging in natural populations of Drosophila melanogaster
12.15-12.35	**Russell Bonduriansky** The final frontier: ageing in wild insect populations
12.35-14.00	*Lunch*
14.00-14.20	**Jean-Michel Gaillard** Reproductive senescence in female large herbivores: a review of the field evidence and some patterns of variation
14.20-14.40	**Alastair Wilson** Support for the evolutionary theory of ageing from two wild vertebrate populations
14.40-15.00	**Jarrod Hadfield** Evolutionary stasis of age-trajectories in a wild population of bird predicted by non-linear developmental processes
15.00-15.20	**Ophélie Ronce** Does dispersal influence the evolution of ageing?
15.20-16.00	*Coffee*

26-01 Talk

POPULATION AGING AND EXTRAORDINARY LIFE SPAN IN WILD MEDFLIES

James R. Carey [1]

[1] *University of California Davis, Entomology, One Shields Avenue, 95616, Davis California, United States*

jrcarey@ucdavis.edu

Although it has been nearly 50 years since the distinguished ecologist LaMont Cole noted that problems involving age distribution in the field are "…*among the most important and least elementary matters with which demographers have to deal*", there is still little known about the age dynamics and life span potential of individuals in wild insect populations. We investigated aging over three field seasons in wild medfly populations in Greece by developing a new approach whereby a demographic deconvolution model and reference life tables are brought to bear on the mortality data gathered from field-captured individuals that were monitored to death in the laboratory. In this talk I will present three components of this overall study. First, the conceptual basis for the use of the death distribution of marked (or captive) individuals of unknown age that we refer to as the 'captive cohort method'. Second, the deconvolution model that reveals a new life table identify whereby the distribution of deaths in a cohort derived from a stationary (life table) population is identical to the age distribution of the population from which they were captured. Third, the empirical findings from the 3-year medfly field study where we estimated age structure and population aging using these methods. I will also discuss the broader, long-term implications of this captive cohort approach including its use in developing a formal demographic framework for capture-recapture methods.

26-02 Talk

PHYSIOLOGICAL EVOLUTION AND RATE OF AGING IN WILD POPULATIONS OF THE GARTER SNAKE (THAMNOPHIS ELEGANS)

Anne M. Bronikowski [1], Kylie Robert [1]

[1] *Iowa State University, Evolution & Organismal Biology, Ames Iowa USA 50011*

abroniko@iastate.edu

Populations of garter snakes (Thamnophis elegans) have been studied in the Northern Sierra Nevada mountain range (USA) since 1976. Through intensive mark/recapture experiments and habitat monitoring, we have reported two ecotypes of garter snake. The fast growth ecotype occurs in low elevation sites in and around a dominant water source; they mature early (2 - 3 years of age), reproduce often (annual litters averaging 7 offspring), and live short lives (median = 4 years of age) in the wild. The slow growth ecotype matures late (5 - 7 years of age), reproduces infrequently and with small litters (average = 3 offspring every 2 or 3 years), and lives longer (median = 8 years); slow growth animals are found in higher elevation mountain meadow sites. Laboratory reciprocal transplant experiments indicate that the fast and slow growth trajectories are due to genetic differences between the two ecotypes. Common garden experiments that test the cellular stress hypothesis of aging reveal that fast growth / short-lived animals: consume more (mass-independent) oxygen over a profile of temperatures; produce greater amounts of mitochondrial ROS per unit time; convert ADP to ATP less efficiently; and lack the ability to repair ionizing damage to DNA to pre-damage (baseline) levels. In all measures, slow growth / long-lived animals outperform the short-lived ecotype. These results suggest that evolution along the physiological axis governing oxygen consumption, mitochondrial function, and DNA repair underlie the evolution of lifespan, growth, and reproduction in these populations of garter snakes.

26-03 Talk

REPRODUCTIVE SENESCENCE IN A LONG-LIVED SPECIES: RATES OF DECLINE IN LATE LIFE PERFORMANCE ARE ASSOCIATED WITH VARYING COSTS OF EARLY REPRODUCTION

Thomas E. Reed [1], Loeske E. B. Kruuk [1], Sarah Wanless [2], Morten Frederiksen [2], Emma J. A. Cunningham [1], Michael P. Harris [2]

[1] *University of Edinburgh, Institute of Evolutionary Biology, Ashworth Laboratories, King's Buildings, Edinburgh EH93JT, UK*
[2] *CEH Banchory, Hill of Brathens, Banchory, AB31 4BW, Aberdeenshire, UK*

tom.reed@ed.ac.uk

Evolutionary theories of senescence predict that rates of decline in performance parameters should be shaped by early-life trade-offs between reproduction and somatic maintenance. We investigated factors influencing the rate of reproductive senescence in a long-lived seabird, the common guillemot *Uria aalge* using data collected over a 23-year period. Guillemots suffered reduced breeding success in the last 3 years of life and females senesced at a significantly faster rate than males. At the individual level, high levels of reproductive output early in life were associated with increased senescence later in life. The rate of senescence was additionally dependent on environmental conditions experienced early in life, with evidence that harsh conditions amplified later declines in breeding success. Early productivity also traded off against lifespan. These results are in line with the antagonistic pleiotropy and disposable soma theories of senescence. We propose that similar studies investigating the importance of such trade-offs under appropriate ecological contexts will further illuminate our understanding of the evolution of senescence.

26-04 Talk

TELOMERE ATTRITION DUE TO CHRONIC INFECTION

Petteri Ilmonen [1], Alexander Kotrschal [1], Dustin J. Penn [1]

[1] *Konrad Lorenz Institute for Ethology, Austrian Academy of Sciences, Savoyenstrasse 1a, 1160 Wien, Austria*

P.Ilmonen@klivv.oeaw.ac.at

Telomeres, the DNA protein complexes at the ends of eukaryotic chromosomes that maintain genomic integrity during mitotic cell division, become shorter with replicative senescence and oxidative stress. Chronic exposure to pathogenic infections is suspected to result in accelerated telomere attrition rate, and a consequent reduction in cellular proliferation rate, which in turn could impair proper immune function and tissue renewal capacity. Pathogen-driven damage to telomeres could thus provide a causal mechanism contributing to immunosenescence and reduced organismal life-span. Correlative studies with humans and short-term antigen stimulation experiments in genetically manipulated mouse strains support this idea, but leave unclear the underlying causal mechanism and applicability of the results to genetically intact hosts/natural pathogen systems. To test this experimentally, we infected wild house mice (*Mus musculus musculus*) with mixed strains of *Salmonella* over seven months, and compared their telomere lengths to sham-infected sibling controls. Our results show that infectious diseases can cause telomere attrition, and suggest that telomere length could provide a molecular marker for individual's exposure and ability to cope with pathogenic insults. We will discuss the implications of these findings for evolutionary theories of aging.

26-05 Talk

REPRODUCTIVE DIAPAUSE AND AGING IN NATURAL POPULATIONS OF DROSOPHILA MELANOGASTER

Paul S. Schmidt [1]

[1] *University of Pennsylvania, Biology, 415 S. University Avenue, 19104, Philadelphia, USA*

schmidtp@sas.upenn.edu

Drosophila melanogaster has been widely used as a model system for the study of aging, but there is relatively little information regarding patterns of aging in natural populations. Across the eastern U. S., six populations were collected and assayed for lifespan, fecundity, and stress resistance. All traits varied predictably with geography: lifespan and stress resistance increased, whereas total and per capita fecundity decreased, with increasing latitude. These patterns may reflect direct or indirect selection by means of underlying genetic correlations. One trait that both varies clinally and impacts aging in flies is reproductive diapause. Diapause expression in D. melanogaster results in lifespan extension, delayed senescence, and increased stress resistance; similarly, the genetic variance for diapause expression also has widespread impacts on life histories. Each of the assayed isofemale lines was phenotyped for diapause and assigned as having a high propensity (diapause genotypes) or a low propensity (nondiapause genotypes) to express diapause. When included as a predictor, diapause genotype explained the majority of the observed variance for lifespan, mortality rates, fecundity profiles, and resistance to cold; geographic origin had a significant effect on heat resistance only. To further examine the impact of reproductive diapause on the variance for aging in natural populations, we examined the effects of naturally occurring alleles at an identified gene for diapause, couch potato (cpo). 10 cpo alleles were placed in a common genetic background and tested over: 1) a gene specific deletion, and 2) a wildtype restoration allele. Both stocks were created by P-element mobilization and are identical except for the gene of interest. The allelic variation segregating at cpo in natural Drosophila populations has a significant impact on the genetic variance for lifespan, mortality rates, fecundity profiles, and patterns of generalized stress resistance.

26-06 Talk

THE FINAL FRONTIER: AGEING IN WILD INSECT POPULATIONS

Russell Bonduriansky [1]

[1] *University of New South Wales, School of BEES, 2052, Sydney NSW, Australia*

r.bonduriansky@unsw.edu.au

It is becoming increasingly clear that a major limitation of our understanding of the evolution of ageing is a lack of knowledge about the expression and fitness consequences of ageing in wild populations. However, research on ageing in wild animals is impeded by logistical challenges whose severity scales inversely with the subjects' body size. Nonetheless, some recent technical and analytical advances have made it possible to begin to uncover patterns of ageing in wild insects. Studies on wild antler flies (*Protopiophila litigata*) provided the first compelling evidence that ageing occurs in wild insect populations, and imposes severe fitness costs. Research on this tiny organism also led to the surprising insight that declining reproductive performance probably imposes far greater fitness costs than declining survival probability, and that the rate of reproductive ageing is positively correlated with body size. Ongoing research focuses on the giant stilt-legged fly *Telostylinus angusticollis*, and the field cricket *Teleogryllus commodus*. Curiously, although these insects are orders of magnitude larger than the antler fly, there is little evidence that they live longer or age more slowly, in contrast with the typical pattern observed in vertebrates. Nonetheless, life history patterns in these wild populations differ strikingly from those of their captive conspecifics, providing a powerful illustration of the effects of environment on the expression of ageing. These studies highlight a number of interesting questions yet to be addressed, and the practical difficulties yet to be overcome, in research on ageing in the wild.

26-07 Talk

REPRODUCTIVE SENESCENCE IN FEMALE LARGE HERBIVORES: A REVIEW OF THE FIELD EVIDENCE AND SOME PATTERNS OF VARIATION

Jean-Michel Gaillard [1], Anne Viallefont [1]

[1] *Université Lyon 1- CNRS, Biométrie et Biologie Evolutive, 43 Bd du 11 novembre 1918, 69622, Villeurbanne, FRANCE*

gaillard@biomserv.univ-lyon1.fr

While evidence of actuarial senescence in large herbivores has accumulated during the last decade thanks to the development of powerful methods of survival analysis, whether the individual reproductive output decreases with increasing age in female large herbivores remains inconclusive. The current view expressed by most investigators is that reproductive senescence could occur, but much later than actuarial senescence, leading the statistical detection quite difficult. Indeed, most data have been collected on shot animals from hunted populations in which only a very small proportion of individuals reach old ages. In addition, such transversal data are likely to underestimate the intensity of senescence because of well-known individual heterogeneities in quality. Taking advantage of the recent availability of detailed individual data collected throughout a long-term monitoring of individuals from birth to death, we tested for reproductive senescence after accounting for possible confounding effects of individual quality. We found that (1) reproductive senescence is pervasive in female large herbivores, (2) the onset of reproductive senescence occurs later than that of actuarial senescence, supporting previous reports from transversal data, and (3) reproductive senescence seems to be more pronounced in populations of large herbivores living under protected environmental conditions (National Parks, unhunted populations) and enjoying long average lifespan. We then discuss the evolutionary consequences of our findings.

26-08 Talk

SUPPORT FOR THE EVOLUTIONARY THEORY OF AGEING FROM TWO WILD VERTEBRATE POPULATIONS

Alastair J. Wilson [1], Daniel H. Nussey [2], Josephine M. Pemberton [1], Tim H. Clutton-Brock [2], Jill G. Pilkington [1], Alison Donald [1], Fanie Pelletier [3], Loeske E. B. Kruuk [1]

[1] *University of Edinburgh, Institute of Evolutionary Biology, West Mains Rd, EH9 3JT, Edinburgh, UK*
[2] *University of Cambridge, Zoology, Downing St, CB23EJ, Cambridge, UK*
[3] *Imperial College London, Biology, Silwood Park, SL5 7PY, Ascot, UK*

alastair.wilson@ed.ac.uk

Current evolutionary theory provides a unifying framework for our understanding the ultimate causes of ageing, but support for the theory comes almost exclusively from a handful of model laboratory study systems. The validity of the evolutionary genetic theory of ageing therefore hinges on the assumption that findings from a handful of laboratory invertebrate populations can be generalised to other taxa and to situations outside the lab. Here we present analyses of age-specific patterns of genetic variance for fitness in two wild ungulate populations to reveal remarkably consistent patterns which support existing evolutionary theory. We show that additive genetic variation (σ^2_A) exists for ageing in both study systems, an assumption of the evolutionary theory of ageing that has yet to be widely tested in nature. We also find evidence that both σ^2_A and inbreeding depression increase with age, thus providing the first evidence in support of the mutation accumulation theory of ageing to come from studies of wild animals in the natural environment.

26-09 Talk

EVOLUTIONARY STASIS OF AGE-TRAJECTORIES IN A WILD POPULATION OF BIRD PREDICTED BY NON-LINEAR DEVELOPMENTAL PROCESSES

Jarrod D. Hadfield [1]

[1] *University of Edinburgh, Ashowrth Labs, EH9 3JT, Edinburgh, UK*

j.hadfield@ed.ac.uk

Aging is a non-linear process often studied in non-Gaussian traits such as survival and fecundity. Using longitudinal data collected on a wild passerine bird I relax the standard assumptions of quantitative genetics (linearity and normality) by imbedding Rice's analytical framework of developmental evolution in an MCMC framework for fitting non-linear genetic models to pedigreed data. Whereas standard quantitative genetic models predict that age-trajectories should be evolving, non-linear developmental models predict evolutionary stasis. This conclusion is consistent with empirical studies of micro-evolution, and phylogenetic studies of macro-evolution. Finally, a meta-analysis demonstrates that the assumptions of this non-linear developmental model are general, and that the standard quantitative genetic framework may be misleading when studying the aging process.

26-10 Talk

DOES DISPERSAL INFLUENCE THE EVOLUTION OF AGING?

Ophélie Ronce [1], Daniel Promislow [2]

[1] *Université Montpellier II CNRS, ISEM UMR 5554, Place Eugène Bataillon, 34095, Montpellier, France*
[2] *University of Georgia, Department of genetics, Life Sciences Building UGA, GA 30602, Athens, USA*

ronce@isem.univ-montp2.fr

Most theory about the evolution of senescence has been elaborated in the context of a very large well mixed population. A few recent models have however shown that spatial structure, metapopulation dynamics and limited dispersal could significantly affect evolutionary trajectories for life history traits such as reproductive effort, age at maturity or life-span (reviewed in [1]). Conversely, patterns of senescence affect the evolution of juvenile dispersal [2]. We here specifically investigate how limited dispersal might influence the evolution of aging. Our analytical model describes how the strength of selection on survival and fecundity changes with age in a patchy population where adults are territorial and a fraction of juveniles disperse between territories. Both parent-offspring competition and sib competition then affect selection on age-specific life history traits. Limited dispersal modifies the strength of selection, its pattern of variation with age, but also its direction. More regular distribution of reproductive events throughout the life is selected for in structured populations than in well-mixed populations. The possibility for the evolution of suicide genes increasing mortality in some age classes with no positive pleiotropic effects on other age classes will be in particular discussed (see also [3]).

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26-01 Poster

EXPERIMENTAL MANIPULATION OF LIFE HISTORY TRAJECTORIES AND RESISTANCE TO OXIDATIVE STRESS

Carlos Alonso-Alvarez [1], Sophie Bertrand [2], Bruno Faivre [3], Gabriele Sorci [3]

[1] *IREC-CSIC, Unidad de Ecologia, Ciudad Real, Spain*
[2] *Universite Paris VI, Lab. Parasitologie Evolutive, Paris*
[3] *Université de Bourgogne, BioGéoSciences, Dijon, France*

carlos.alonso@uclm.es

Evolutionary theory tells us that optimal investment in reproduction versus maintenance is likely to shape the pattern of age-associated decline in performance, also known as aging. The currency that is traded against different vital functions is still debated. Here, we took advantage of a phenotypic manipulation of individual quality in early life to explore (1) long-term consequences on life-history trajectories, and (2) the possible physiological mechanism underlying the life-history adjustments. We manipulated phenotypic quality of a cohort of captive zebra finches (*Taeniopygia guttata*) by assigning breeding pairs to either an enlarged or a reduced brood. Birds from enlarged broods delayed reproduction. Birds that delayed reproduction produced less offspring but lived longer, although neither fecundity nor longevity were directly affected by the experimental brood size. Birds raised in reduced broods tended to have a higher population growth rate, and a steeper decrease of reproductive value with age than birds reared in enlarged broods. Metabolic resources necessary to fight off the damaging effect of reactive oxygen species (ROS) could be the mechanism underlying the observed results, as (1) birds that engaged in a higher number of breeding events had a weaker red blood cell resistance to oxidative stress, (2) red blood cell resistance to oxidative stress predicted short-term mortality (but not longevity), and (3) was related with a parabolic function to age. Overall, these results suggest that the trade-off between reproduction and self-maintenance might be mediated by the cumulative deleterious effect of ROS.

26-02 Poster

INDIVIDUAL PATTERNS OF REPRODUCTIVE SENESCENCE IN GREAT TITS

Sandra Bouwhuis [1], Ben C. Sheldon [2], Simon Verhulst [1], Anne Charmantier [3]

[1] *University of Groningen, Behavioural Biology Group, Kerklaan 30, 9751NN, Haren, The Netherlands*
[2] *University of Oxford, Edward Grey Institute, South Parks Road, OX13PS, Oxford, United Kingdom*
[3] *CNRS, Centre for Functional and Evolutionary Ecology, 1919 Route de Mende, F34293, Montpellier, France*

a.h.j.bouwhuis@rug.nl

Understanding the factors associated with the evolution of senescence is a major goal in evolutionary biology. An important first step towards this goal is to quantify rates of senescence. Because senescence refers to phenotypic changes with age within individuals, this requires longitudinal data as well as the ability to separate within- from between-individual effects. This has rarely been achieved for natural populations. We applied a mixed model analysis to 45 years of data from a wild population of great tits at Wytham (Oxfordshire, UK). For this population, cross-sectional analyses have previously shown a decline in some aspects of reproductive performance with age at the population level. Using almost 10,000 records from individual breeders of 1 to 8 years of age, we separate contributions of within-individual change and selective disappearance underlying these population patterns. We show important senescent declines in individual performance after 4 years of age for reproductive traits, such as laying date and clutch size, as well as fitness proxies, such as number of offspring recruited to the population. As a second step towards our goal of identifying factors associated with the evolution of senescence, we investigate which parts of the breeding cycle are especially prone to age-specific declines and test for effects of sex, social status and early conditions.

26-03 Poster

EVOLUTION OF COGNITIVE SENESCENCE

Joep M. S. Burger [1], Juliette Pont [1], Tad J. Kawecki [1]

[1] *University of Fribourg, Unit of Ecology and Evolution, Chemin du Musée 10, CH1700, Fribourg, Switzerland*

jozef.burger@unifr.ch

It has long been appreciated both verbally and mathematically that the strength of selection declines with age. As a result, genes with deleterious effects late in life can become fixed in a population if they have neutral or beneficial effects early in life. This can explain the evolution of senescence, i.e. the age-related decrease in survival and function. It remains unclear, however, how demographic and functional senescence are genetically linked. To address this problem, we studied demographic and functional senescence using two manipulations that extend life span in *Drosophila*: selection for late-life fecundity and ablation of cells that produce insulin-like peptides. We measured olfaction and memory as functional traits. The results provide an important step towards understanding the evolution of cognitive senescence.

26-04 Poster

EFFECTS OF EARLY RESOURCE LIMITATION AND COMPENSATORY GROWTH ON LIFETIME FITNESS IN THE LADYBIRD BEETLE (HARMONIA AXYRIDIS)

Caitlin M. Dmitriew [1], Locke Rowe [1]

[1] *University of Toronto, Department of Ecology and Evolutionary Biology, 25 Harbord St., M5S3G6, Toronto, Canada*

dmitriew@zoo.utoronto.ca

Acceleration of growth following a period of diet restriction may result in either complete or partial catch-up in size. The existence of such compensatory growth indicates that organisms commonly grow at rates below their physiological maxima and this implies a cost for accelerated growth. We examined patterns of accelerated growth in response to temporary resource limitation, and assayed both short and long-term costs of this growth in the ladybird beetle Harmonia axyridis. Subsequent to the period of food restriction, accelerated growth resulted in complete compensation for body sizes, although we observed greater larval mortality during the period of compensation. There were no effects on female fecundity or survivorship within three months of maturation. Females did not discriminate against males that had undergone compensatory growth, nor did we observe effects on male mating behaviour. However, individuals that underwent compensatory growth died significantly sooner when deprived of food late in adult life, suggesting that longer-term costs of compensatory growth may be quite mild and detectable only under stressful conditions.

26-05 Poster

NUTRITIONAL STRESS, GENETIC VARIATION AND THE TICKING OF THE BIOLOGICAL CLOCK IN COCKROACHES

Martin Edvardsson [1], John Hunt [1], Allen J. Moore [1], Patricia J. Moore [1]

[1] *University of Exeter, School of Biosciences, Cornwall Campus, TR10 9EZ, Penryn, UK*

M.Edvardsson@exeter.ac.uk

Loss of fertility appears to happen independently of somatic senescence in females of some species including humans. Whether early cessation of reproduction is adaptive or simply the result of weak selection on offspring production late in life has been the subject of much debate. Females of the cockroach *Naphoeta cinerea* have a limited supply of oocytes, produce discrete clutches of live born offspring and sometimes stop reproducing long before they die. Virgin females lose oocytes through apoptosis. It has been suggested that insects may sacrifice oocytes in this way to recycle nutrients thus trading fertility for survival in times of starvation. We studied quantitative genetic variation underlying individual expression of apoptosis in oocytes of more than 1200 virgin *N. cinerea* under conditions of excess and restricted food. Mean levels of apoptosis increased when food was limited. There was little genetic variation in levels of apoptosis under excess food but substantial additive genetic variation under restricted food. Our study is the first to demonstrate quantitative genetic variation in the regulation of apoptosis in any animal. The results show that the ticking of the biological clock in virgin cockroaches depends on an interaction between the genotype and the environment; some individuals are more prone to lose their oocytes than others when food becomes limited. Preliminary results from our ongoing study indicate that the way apoptosis is regulated in oocytes has important effects on female lifetime reproductive success.

26-06 Poster

AGEING PATTERN IN THE FRESHWATER SNAIL PHYSA ACUTA: SUPPORT FOR THE MUTATION-ACCUMULATION THEORY

Juan S. Escobar [1], Philippe Jarne [1], Patrice David [1]

[1] *Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), UMR 5175 CNRS, 1919 Route de Mende, 34293, Montpellier Cedex 5, France*

escobar@cefe.cnrs.fr

Senescence is the process of intrinsic deterioration that is characterized by a decrease of survival and a decline in offspring production with time. Two main theories – mutation accumulation (MA) and antagonistic pleiotropy (AP) – have been proposed to account for its evolution. Under MA, mutations acting late in life reach higher frequencies at mutation-selection balance because the efficiency of selection decreases with age. One expects then an increase of both inbreeding depression and genetic variance with age. Under AP, mutations that produce beneficial effects early in life, but that later increase the rate of ageing, can be maintained in populations because selection will act more strongly on the early beneficial effect than on the later deleterious one. Under AP one expects a negative association between traits that express early and late in the life cycle. We studied the ageing pattern for survival and fecundity in the freshwater snail *Physa acuta* using a large quantitative genetics design (36 grand-families, 348 second-generation families and more than 2000 third-generation offspring). We examined the timing and magnitude of inbreeding depression across a full life-cycle, as well as changes in genetic variance. Our results show that inbreeding depression significantly increases with age for both survival and fecundity. Moreover, the familial (genetic) variance for inbreeding depression increases with age and we found no evidence of negative genetic correlations between early and late expressing characters. These results support the expectations of the MA theory, while the main prediction of AP theory was not met. This is to our knowledge the first test of evolutionary theories of senescence in invertebrate models other than *Drosophila* and *Caenorhabditis elegans*.

26-07 Poster

AGING & REPRODUCTIVE STATUS IN EURASIAN BADGERS

Melissa R. Gunn [1], Gavin Wilson [1], Richard Delahay [1]

[1] *Central Science Laboratories, CSL Woodchester park, Tinkley Lane, GL10 3UJ, Nympsfield, UK*

m.gunn@csl.gov.uk

The effects of age on reproductive function are important features in population dynamics and play a major role in life-history evolution. The Eurasian badger (Meles meles) is a long-lived mammal that lives in social groups in the much of the UK. Here we discuss findings from a 30-year mark-recapture study of wild badgers in the south of England. Multiple records of reproductive status are available for both males and females of known age during this period. There is evidence for reproductive senescence in this population, with no reproductively active females recorded after 12 years of age, although the oldest badgers are 14. Survival probability also decreased with age from about 8 years. We have used a linear mixed model approach to determine what factors affect female reproductive status. Age, season, social group and identity all significantly affected reproductive status. We will discuss the effects of age at first reproduction upon longevity. We aim to combine this data with a quantitative genetic approach in order to determine the evolutionary effects of reproduction in this population of badgers.

26-08 Poster

OLDER MALES SIRE OFFSPRING OF SUPERIOR GENETIC QUALITY IN BROWN TROUT (SALMO TRUTTA)

Alain Jacob [1], Jean-François Rubin [2], Claus Wedekind [1]

[1] *University of Lausanne, Department of Ecology and Evolution, Biophore, 1015, Lausanne, Switzerland*
[2] *Ecole d'ingénieurs HES, Centre de Lullier, 1254, Jussy, Switzerland*

alain.jacob@unil.ch

It is still unclear whether old males should be expected to be of better genetic quality as breeders than young males. On the one hand, older males may be of high genetic quality because they are the ones who survived. On the other hand, however, an accumulation of germ-line mutations over time may continuously reduce the genetic quality of old males' sperm, which may reduce offspring survival. We drew random samples of mature male Brown trout from wild populations and used behavioural observations in an experimental spawning channel to determine their dominance hierarchy in intra-sexual competition, and the traits linked to dominance. We then used sperm of several samples of males for in vitro fertilisation in full-factorial crossings (North-Carolina II design) and raised the resulting embryos at different levels of experimentally induced stress. Embryo survival was used as a measure of male genetic quality. We also determined additive genetic, non-additive genetic, and maternal-environmental effects on embryo survival. We found that older and larger males are more dominant and that males differ significantly in their genetic quality. Embryo mortality at benign conditions was not linked to any sire traits. However, the offspring of old males survived better under stressful conditions than the offspring of younger males. This suggests that females can improve the genetics of their offspring by mating with old and dominant males.

26-09 Poster

TELOMERES – A BIOMARKER FOR STRESS RATHER THAN FOR AGE

Alexander Kotrschal [1], Petteri Ilmonen [1], Dustin J. Penn [1]

[1] *Austrian Academy of Sciences, Konrad Lorenz Institute for Ethology, Savovenstrasse 1a, 1160, Wien, Austria*

kotrschal@esh.unibe.ch

Telomeres, DNA–protein complexes at the ends of chromosomes that control genomic integrity, appear to become shorter with age. Telomere length has been suggested to provide a biomarker for determining the age of wild animals, but only with varying success. Correlative evidence suggests exposure to chronic stress is one of the reasons for telomere attrition and we tested this idea experimentally. We exposed the offspring of wild-caught house mice (*Mus musculus*) to stressful conditions and examined the changes in telomere length over six months. We found that females exposed to males and reproductive stress (either with or without crowding) had significantly shorter telomeres than controls, and males exposed to crowding stress had shorter telomeres than males that were not crowded. Our results indicate that stress alters telomere dynamics, causing attrition and hindering restoration, and these effects are sex dependent. Rather than providing an indicator for chronological age, telomeres may provide a better biomarker for assessing an individual's cumulative exposure or ability to cope with stressful conditions, or their biological age.

26-10 Poster

DETERMINANTS OF QUALITY IN A LONG LIVED COLONIAL SPECIES

Sue Lewis [1], Sarah Wanless [2], David A. Elston [3], Mike P. Harris [2]

[1] *University of Aberdeen, School of Biological Sciences, UK*
[2] *CEH Banchory, UK*
[3] *BIOSS, Macaulay Institute, UK*

s.lewis@abdn.ac.uk

In many animal populations a small proportion of individuals are responsible for producing the majority of surviving offspring, but the underlying mechanisms remain unclear. The role of behaviour in determining variation in 'individual quality' was examined using the common guillemot *Uria aalge*, a monogamous seabird with bi-parental care. Using a novel mixed model approach, a quality estimate was derived for each breeding individual and pair from a model containing variables critical to breeding success. The probability of a successful reproductive attempt was explained by the timing of breeding, age, successful breeding experience and number of mates. Behavioural traits associated with incubation and chick rearing were examined in relation to these quality estimates. Behaviour was an important proximate mechanism underlying quality, in particular the foraging abilities of the pair, and the female's contribution to offspring provisioning. In species with bi-parental care, behavioural correlates of quality operate most strongly at the scale of the breeding pair, since contributions from both individuals are required for a successful outcome.

26-11 Poster

MITOCHONDRIAL MUTATION RATE VARIATION AND THE BIOLOGY OF AGEING IN MAMMALS.

NABHOLZ Benoit [1], GLEMIN Sylvain [1], GALTIER Nicolas [1]

[1] *University Montpellier II, Institut des Sciences de l'Evolution, Place E. Bataillon, 34095, Montpellier - cedex 5, France*

bnabholz@univ-montp2.fr

In the mid-1950s, Denham Harman articulated a 'free-radical theory' of human ageing, speculating that endogenous oxygen radicals were generated in cells and resulted in a pattern of cumulative damage (Harman 1957). This theory has been supported by, e.g., the report of an inverse correlation between oxydative damage marker concentration and maximum life span in mammals (Barja and Herrero 2000). The current interpretation of the 'free-radical theory' of ageing links this pattern with the main source of oxygen free radicals in the body - mitochondrial respiration. The production of free radicals occurs primarily in the electron transport chain complexes. Thirteen of the proteins composing these complexes are encoded by mitochondrial DNA (mtDNA). The mitochondrial theory of ageing postulate that mutations occuring on mtDNA, by affecting the efficiency of respiratory proteins, result in an increase of the rate of free-radical likeage, which in turn increases the mutation rate – a positive loop eventually resulting in ageing. Given the functional implication of mtDNA in ageing, it is therefore tempting to relate the well-documented hypermutability of mtDNA in animals (e.g. Galtier et al 2006) to the existence of a senescing soma: the mtDNA mutation rate might be optimized to confer organisms their appropriate life time, a hypothesis we address in this work. Taking mammals as model taxa, we estimated the mtDNA mutation rate for ~450 species. Our analysis reveals that mtDNA mutation rate is negatively correlated to generation time and maximal life span and is consistent with the hypothesis of a selected reduction of mtDNA mutation in relation to increased longevity in mammals.

26-12 Poster

LONGEVITY DUE TO INTEGRATION OF A MITOCHONDRIAL PLASMID INTO THE MITOCHONDRIAL GENOME

Bart P. S. Nieuwenhuis [1], Anne D. Van Diepeningen [1], Yanan Wang [1], Marijke Slakhorst [1], Alfons J. M. Debets [1]

[1] *Wageningen University, Evolutionary Genetics, Arboretumlaan 4, 6703 BD, Wageningen, The Netherlands*

bart.nieuwenhuis@wur.nl

Aging in the filamentous fungus *Podospora anserina* is associated with instability of mitochondrial DNA (mtDNA). In natural populations a senescence related plasmid pAL2-1 occurs in ~30% of the isolates. pAL2-1 reduces lifespan of the fungus and makes it insensitive for prolonged life due to catabolite restriction. The reduced lifespan appears to be caused by insertion of the plasmid into the mtDNA thereby decreasing stability of the mitochondria. However, integration of the plasmid can also have a positive effect on lifespan. Insertions of the plasmid can stabilize the mitochondria and reduce known characteristics of senescence. In this research we conducted a systematic investigation of long living mutants with pAL2-1 insertion in the mtDNA, the molecular background of the insertion and its effects on longevity under normal and calorie restricted conditions.

26-13 Poster

SOURCES OF INDIVIDUAL HETEROGENEITY INFLUENCING AGE-SPECIFIC REPRODUCTION AND SURVIVAL IN NATURAL POPULATIONS OF VERTEBRATES

Ulrich K. Steiner [1], Shripad Tuljapurkar [1]

[1] *Stanford University, Biological Sciences, 94305, Stanford, CA, United States*

orzack@freshpond.org

We investigated the influence of dynamic heterogeneity and of fixed heterogeneity on the distribution of lifetime reproductive success in natural populations of vertebrates. Using longitudinal mark-recapture data, we calculated age-specific survival rates as well as transition rates between different reproductive strata (levels of reproductive performance) in order to calculate a distribution of lifetime reproductive success uninfluenced by fixed individual-level heterogeneity. We then compared this distribution with the observed distribution of lifetime reproductive success, which is possibly influenced by such heterogeneity, so as to assess the relative support for dynamic heterogeneity and for fixed heterogeneity. One of the species showed only dynamic heterogeneity. The others showed both types of heterogeneity, with dynamic heterogeneity explaining more variance in lifetime reproductive success than fixed heterogeneity. We further compared variability of lifetime reproductive success within and between simulated life-history trajectories. For most species, variability within trajectories was substantially greater than variability between trajectories suggesting that these species are at or near selective equilibrium with respect to lifetime reproductive success; differences in the age of onset of reproduction and in the frequency of reproduction do not appear to explain the large variability between life history trajectories.

26-14 Poster

ANALYSIS OF THE STATICS AND DYNAMICS OF REPRODUCTION AND SURVIVAL IN NATURAL POPULATIONS: SENESCENCE AS PATTERN AND AS EVOLUTIONARY PROCESS

Steven Orzack [1], Ulrich K. Steiner [2], Shripad Tuljapurkar [2]

[1] *Fresh Pond Research Institute, 173 Harvey Street, 02140, Cambridge, MA, USA*
[2] *Stanford University, Biological Sciences, 94305, Stanford, CA, United States*

orzack@freshpond.org

We analyzed age-dependent reproduction and survival in a wide variety of bird and mammal species that exhibit apparent senescence of age-specific survival rates. We show that in most of these species the interaction between reproduction and survival is such that survival rates contingent upon reproduction need not exhibit senescence and that reproduction and survival at any one time may have a positive “static” association. Analysis of the stochastic process describing changes between reproductive strata (levels of reproduction) indicated that the half-life of stratum-residence time is much shorter than the modal and average reproductive lifetimes. This suggests that stratum dynamics act to disconnect reproduction and survival over the lifetime of most individuals and that an underlying negative association or trade-off between these traits need not be invoked in order to explain a positive static association between reproduction and survival. These results underscore the necessity of distinguishing between pattern and process when assessing the degree to which there is senescence in natural populations. No answer to the pattern question “Do the age-specific survival rates decline at an accelerating rate?” can by itself answer the process question as to whether there is senescence. Our results illustrate the need to study the statics and dynamics of reproduction and survival in natural populations.

26-15 Poster

FUNCTIONAL SIGNIFICANCE OF ALLELIC VARIATION AT A CANDIDATE GENE FOR AGING IN DROSOPHILA

Annalise B. Paaby [1], Paul S. Schmidt [1]

[1] *University of Pennsylvania, Department of Biology, 415 S. University Avenue, 19104, Philadelphia, PA, USA*

paaby@sas.upenn.edu

Organism lifespan is a complex quantitative trait, with both genetic and environmental determinants. Several candidate genes for aging have been identified in D. melanogaster by extended longevity mutant phenotypes. One such gene, methuselah (mth), has shown significant genetic variation, evidence of differential selection across environmental heterogeneity, and evidence of rapid protein evolution in natural populations along the U.S. east coast. Wild populations of D. melanogaster also show changing patterns of longevity, fecundity and stress resistance across this latitudinal gradient. We hypothesize that shifting selection pressures across this heterogeneous environment are driving alternative life histories and that mth may be an important target in this regime. But does allelic variation at mth contribute to functional differences in phenotype? This question is critical to understanding how genes influence lifespan determination and how longevity phenotypes have evolved. Here I present data demonstrating that wild mth alleles show significant functional differences in stress resistance, fecundity and lifespan.

26-16 Poster

EVIDENCE OF AGE-SPECIFIC FAMILY EFFECTS AND HERITABILITY IN FECUNDITY OF PRE-INDUSTRIAL FINNISH WOMEN

Jenni E. Pettay [1], Anne Charmantier [2], Virpi Lummaa [3]

[1] *University of Turku, Section of Ecology, Department of Biology, University of Turku, 20014, Turku, Finland*
[2] *Centre Ecologie Fonctionnelle et Evolutive, Département Biologie des Populations, UMR CNRS 5175, 1919 route de Mende, 34293, Montpellier, France*
[3] *University of Sheffield, Department of Animal and Plant Sciences, Sheffield S10 2TN, S10 2TN, Sheffield, United Kindom*

jenni.pettay@utu.fi

A population's potential for evolutionary change depends on the amount of genetic variability expressed in traits under selection. Studies attempting to measure this variability typically do so over the lifespan of individuals, but theory suggests that the amount of additive genetic variance can change during the course of individuals' lives. Here we use pedigree data from historical Finns and the 'Animal Model' to investigate how female fecundity, throughout an individual's reproductive life, is influenced by 'maternal' (family) versus additive genetic effects. We show that while 'family' effects explain variation in female fecundity early in life, these effects wane with female age. Moreover, this decline in family effects is associated with a concomitant increase in additive genetic variance with age. Our results thus highlight that single over-lifetime estimates of trait heritability may give a misleading view of a trait's potential to respond to changing selection pressures.

26-17 Poster

WHY BUTTERFLIES ARE LIKE TORTOISES AND MAYFLIES: THE ROLE OF PHENOTYPIC PLASTICITY IN THE EVOLUTION OF AGEING

Jeroen Pijpe [1], Paul M. Brakefield [2], Bas J. Zwaan [2]

[1] *Leiden University Medical Center, Human Genetics, Einthovenweg 20, 2333 ZC, Leiden, the Netherlands*
[2] *Leiden University / IBL, Evolutionary Biology, Kaiserstraat 63, 2311 GP, Leiden, the Netherlands*

j.pijpe@lumc.nl

To fully understand variation in ageing, including in humans, we need to study ageing in the context of the ecology and selection in the field, *i.e.* in natural populations. In the present study, we investigate how the genetics underpinning variation in ageing is embedded in a life history that is dominated by phenotypic plasticity. The tropical butterfly species *Bicyclus anynana* has evolved phenotypic plasticity to adapt as adults to the alternating wet and dry seasons it encounters. This has resulted in two alternative life histories: in the wet season, butterflies are short-lived and reproduce rapidly; in the dry season, butterflies are long-lived and postpone reproduction many months until the next wet season. We use an integrative approach that combines experimentation in the laboratory using stocks that capture the natural genetic variation for the relevant traits with extensive knowledge of the field biology. We present data from a population that was subjected to artificial selection in wet season conditions for increased starvation resistance, a trait closely related to fitness in the dry season and strongly correlated to ageing. The data include a range of correlated traits under various relevant environmental conditions, from expression of candidate ageing genes, to egg size, metabolic rate, and mating success. From all these traits it emerges that the selected phenotype strongly resembles the dry season form that normally only results from the environmental conditions that prevail in the stress-full dry season. We conclude that the evolution of longevity and other ageing-related traits can only be understood in the light of the natural life history configuration and its related ecology. Finally, we postulate that in this species the mechanisms of ageing are to a large extent plastic, and may underlie adaptive phenotypic plasticity to variable environmental conditions, within an individual's lifespan, as well as over generations. This notion may well be true for other species, including humans.

26-18 Poster

TELOMERE SHORTENING IN JACKDAWS, A LONGITUDINAL STUDY

Martijn Salomons [1], Ellis Mulder [1], Louis Van de Zande [2], Simon Verhulst [1]

[1] *University of Groningen, Behavioural Biology, POBox 14, 9750 AA, Haren, The Netherlands*
[2] *University of Groningen, Evolutionary Genetics, POBox 14, 9750 AA, Haren, The Netherlands*

h.m.salomons@rug.nl

Telomeres are highly repeated DNA sequences at the ends of linear chromosomes. Telomeres shorten with age and the rate of telomere shortening is higher in species with short maximum lifespan. A mechanism explaining this pattern is that telomere shortening rate behaves as an index of the accumulation of oxidative stress related damage. The majority of studies on age related telomere length are based on cross-sectional analyses of telomere length. Therefore it is possible that the observed differences in telomere length between old individuals and younger individuals could be confounded by selective disappearance, when individuals with short telomeres have a higher mortality risk.

In this study we show three years of longitudinal data on telomere shortening in individual jackdaws varying in age (range: 1-12). We find that telomere shortening rate estimated using longitudinal data was much steeper than an estimate based on cross-sectional data, suggesting selective disappearance of individuals with short telomeres. Furthermore, we find that shortening rates vary between different parts of the telomere length distribution. Within individuals, longer telomeres shorten at a higher rate than shorter telomeres. We theoretically examine different shortening mechanisms that explain this pattern.

26-19 Poster

INTRA-SPECIFIC VARIATION IN LIFE-HISTORY TRAITS AMONG WILD POPULATIONS OF *CAENORHABDITIS ELEGANS*

Fiona R. Savory [1], Steve M. Sait [1], Ian A. Hope [1]

[1] *University of Leeds, Biology, L.C.Miall Building, University of Leeds, LS2 9JT, Leeds, UK*

bsfrs@leeds.ac.uk

The standard laboratory strain of *Caenorhabditis elegans* is extensively employed as a model for ageing research. However, this strain was maintained in culture for over a decade after being isolated from its natural environment and may thus have lost some genetic and phenotypic characteristics representative of the original wild population. In order to investigate the role of ecological and evolutionary processes involved in ageing, and to characterise senescence and related life-history traits as they may be expressed in nature, recently isolated wild populations were compared and contrasted with the standard laboratory strain. We describe intra-specific variation in senescence, age at first reproduction, fecundity and population growth rate, and relationships between these traits.

26-20 Poster

DEVELOPMENTAL CONDITIONS INFLUENCE ADULT LONGEVITY IN THE COLLARED FLYCATCHER.

Joanna Sendecka [1], Lars Gustafsson [1]

[1] *Uppsala University, Animal Ecology, Norbyvägen 18D, 75236, Uppsala, Sweden*

joanna.sendecka@ebc.uu.se

Longevity is one of the major factors determining lifetime reproductive success in birds and many other animals and plants. It has been shown to be related to individual quality, but the factors directly determining individual lifespan in the wild are still not clear. Using long-term data collected during 25 years, we investigated possible factors influencing longevity of female collared flycatchers, by comparing multiple characters of short and long-lived individuals, including conditions during growth and development and future reproductive decisions as adult. The parameters best explaining differences in longevity of female collared flycatchers are their body mass and tarsus length as a fledgling, the attractiveness (forehead patch) of their father and the attractiveness of their partners. Fledgling tarsus length and father's forehead patch size had positive effects on female longevity, whereas fledgling body mass and partner's forehead patch had negative effects on female longevity. Thus, female longevity can be predicted both from their condition as nestlings and from reproductive decisions later in life. The negative correlation between female longevity and its body mass as a fledgling, although very strong as based on a big sample size, is in a contrary to the previous findings and expectations for passerine birds. It can be explained by two alternative mechanisms. According to the first explanation, long-lived females experienced very good developmental conditions, which resulted in their fast growth and development. Alternatively, as lifespan have been shown before to be prolonged by calorie restriction, relatively low but stable food condition could also create the observed pattern. In the situation of relatively low food conditions, an individual is expected to invest more into self-maintenance and less into fattening, which is in accordance to the observed correlation between female longevity and its body size and mass as fledging. Our study is the first one showing possible mechanism of the influence of calorie restriction on longevity in the wild bird.

26-21 Poster

SENESCENCE AND REJUVENATION IN THE FILAMENTOUS FUNGUS PODOSPORA ANSERINA

Anne D. Van Diepeningen [1], Alfons J. M. Debets [1], Rolf F. Hoekstra [1]

[1] *Wageningen University, Genetics, Arboretumlaan 4, 6703BD, Wageningen, The Netherlands*

anne.vandiepeningen@wur.nl

Biological ageing is controlled by a complex network of molecular pathways and interactions. Mitochondria, the organelles of energy transduction, play a major role in this network, which may be related to the production of reactive oxygen species (ROS) as Harman's free radical theory of ageing suggests or due to other mechanisms. We are still far from understanding the details about the precise mechanisms how mitochondria and interactions of these organelles with other cellular compartments and the environment are involved in the control of life span and ageing.

Filamentous fungi are modular organisms and as such not expected to age and most don't. However, *Podospora anserina* has a long history in experimental ageing research and a well demonstrated mitochondrial etiology of ageing. Coprophilous *P. anserina* is characterized by a genetically controlled short life span (approx. 25 days) and a short generation time (approx. 14 days). Classical genetic experiments revealed a clear genetic basis of ageing and specifically the involvement of extrachromosomal genetic factors in *P. anserina*. The demonstration that mitochondrial inhibitors affect life span clearly pointed to mitochondria as the cellular compartment involved in the control of the ageing process. Subsequently, molecular analyses revealed age-dependent reorganizations of the mitochondrial DNA (mtDNA) playing a central role in ageing of *P. anserina* wild-type cultures.

Ascospores produced on a (pre-) senescent culture will often display a juvenile phenotype (a phenomenon termed *rejuvenation*). To study whether and how this rejuvenation occurs, a comparison was made between the fitness of spores and the fitness of the mycelium. A full grown mycelium was sampled at five different time points during its lifespan and both samples of the mycelium and of produced ascospores were tested in turn for their lifespan. The results suggest intra-organismal selective access of functional juvenile mitochondria to reproductive structures.

26-22 Poster

SEX-DEPENDENT AGEING IN A WILD POPULATION OF CRICKETS

Felix Zajitschek [1], Russell Bonduriansky [1], Chad Brassil [2], Robert Brooks [1]

[1] *University of New South Wales, School of Biological, Earth and Environmental Sciences, 2052, Sydney, Australia*
[2] *University of Nebraska, School of Biological Sciences, NE 68588-0118, Lincoln, USA*

felix.zajitschek@student.unsw.edu.au

Most research on the evolutionary biology of ageing has been done in the laboratory, where natural selection pressures are eliminated or manipulated, so that there is little information on how and even whether organisms age in the wild where they experience the full range of mortality hazards under which they have evolved. This is especially true for short-lived and difficult to monitor species like most insects. Here we test ageing in a natural population of black field crickets, Teleogryllus commodus. By analyzing a capture-recapture study using innovative non-parametric methods for obtaining lifetable parameters, we show that mortality rates not only increase with increasing age, which is a signature of ageing, but that there are also differences in mortality patterns between male and female crickets. This finding is corroborated by results from an experiment in field enclosures, where mortality rate increased with increasing age, but with an earlier onset of mortality in males compared to females. This means that crickets in this natural population show a senescent pattern of age-specific mortality. The fact that males and females express different age-dependent ageing-phenotypes suggests that there should exist sex-specific optima in the timing of resource allocation to somatic maintenance and reproductive effort.

Evolutionary histories beyond organelle DNA

27

Friday August 24 *Location*: University building X

Symposium 27: Evolutionary histories beyond organelle DNA

Organizers: Gerald Heckel, University of Bern, Switzerland
Maarit Jaarola, University of Lund, Sweden

9.45-10.15	**Kerry Shaw** (invited) Gene trees in recent species radiations
10.15-10.45	**Rémy Petit** (invited) Reconstructing plant evolutionary histories: what are organelle genes good at?
10.45-11.05	**Tor Carlsen** Combining AFLPs, SSRs, and plastid and nuclear sequences in phylogeography and systematics
11.05-11.35	*Coffee*
11.35-11.55	**Maxim Kapralov** Positive selection facilitates interspecific gene transfer in Hawaiian endemic Schiedea
11.55-12.15	**Graham Muir** A selective sweep in the chloroplast DNA of dioecious Silene (section Elisanthe)
12.15-12.35	**Stéphane Hemmerter** A curious coincidence: mosquito biodiversity and the limits of the Japanese encephalitis virus in Australasia
12.35-14.00	*Lunch*
14.00-14.20	**Zuzana Musilova** Incomplete lineage sorting or hybridisation? Multilocus phylogeny and coalescent simulation suggest introgressive hybridisation in asexual complex of European loaches
14.20-14.40	**Nabholz Benoit** Determinism of mitochondrial genetic diversity in birds and mammals
14.40-15.00	**Patricia Brito** Speciation history of white-eyes (Zosterops griseotinctus) complex in the Solomon archipelago: contrast between anonymous nuclear loci and mtDNA
15.00-15.20	**Pierre-André Crochet** When mtDNA is not enough: conflicts among markers reveal misleading mtDNA histories
15.20-16.00	*Coffee*

27-01 Talk

GENE TREES IN RECENT SPECIES RADIATIONS

Kerry L. Shaw [1]

[1] *University of Maryland, Biology, Biology/Psychology Building, 20742, College Park, Maryland, USA*

kerryshaw@umd.edu

There are several ways in which gene trees will not completely represent species trees. These discrepancies may be due to, for example, gene lineage sorting, gene duplication, or hybridization leading to "interspecific" gene flow. I will discuss the kinds of evolution, including morphological, behavioral and gene-genealogical changes, that are likely at the level of recently diverging species. One manifestation of this complex evolution is the recent production of numerous species concepts. To many, this has rocked the foundations of systematics and evolutionary biology. However, to the speciation biologist, this is a productive time and species concepts can be seen as models invoked to "explain" and/or organize the diversity natural evolutionary groups. Isolated biotas on island archipelagos and lake systems frequently harbor recent species radiations. Features of such radiations, such as varying degrees of sympatry and allopatry and the tendency to hybridize, offer excellent natural systems in which to examine the complexities of species. I will illustrate some of these complexities in part through a discussion of Hawaiian crickets of the genus Laupala.

27-02 Talk

RECONSTRUCTING PLANT EVOLUTIONARY HISTORIES: WHAT ARE ORGANELLE GENES GOOD AT?

Rémy J. Petit [1]

[1] *INRA, UMR1202 Biogeco, 69 route d'Arcachon, 33610, Cestas, France*

petit@pierroton.inra.fr

Organelle DNA (chloroplast and mitochondrial DNA) surveys still dominate phylogeographic studies in plants. This might seem surprising because these genomes are typically characterised by low rates of variation compared to nuclear genes and because they represent a single uniparentally inherited locus, making it difficult to appreciate the true stochasticity of the underlying processes. Nevertheless, they have remained very popular because of the strong geographic patterns they often reveal. Using case studies, I will illustrate some of the risks of relying solely on organelle markers, including in situations where they are usually considered to be particularly well suited (e.g. the reconstruction of historically contingent colonisation routes). Conversely, I will stress the benefits of including them in situations where they are considered to be misleading (e.g. studies of species delimitation and introgression). Altogether, and not surprisingly, I conclude that organelle genes remain irrepleacable and are still a source of inspiration, as pointed early by John Avise, but that they are best utilized in conjunction with nuclear markers.

27-03 Talk

COMBINING AFLPS, SSRS, AND PLASTID AND NUCLEAR SEQUENCES IN PHYLOGEOGRAPHY AND SYSTEMATICS

Tor Carlsen [1], Pernille B. Eidesen [1], Reidar Elven [1], Christian Brochmann [1]

[1] *University of Oslo, National Centre for Biosystematics, Natural History Museum, P.O. Box 1172 Blindern, Oslo, Norway*

torac@nhm.uio.no

Unravelling the evolutionary history of young taxa can be an expensive and tedious task. Even extensive search for variation can fail to provide well-supported groups when using only one marker system (such as sequencing of plastid regions). In two studies, we combined high-resolution multilocus genotyping (AFLPs and SSRs) with more slowly evolving introns and intergenic spacers from plastid and nuclear genomes. For the genus *Smelowskia*, seven SSR loci combined with two nuclear regions (RPA2 intron 23 and nrITS) and five plastid regions (*trn*L^{UAA} and *rp*S16 introns, *trn*H^{GUG}-*psb*A, *trn*L^{UAA}-*trn*F^{GAA}, and 5'*rp*S12-*rp*L20 spacers) were needed to separate individual species and for phylogenetic/biogeographic inference. In *Cassiope tetragona*, AFLPs combined with sequencing of plastid regions supported the current subspecies classification and provided evidence for a recent circumpolar expansion out of Beringia for subspecies tetragona. These studies demonstrate that a combination of different marker systems can complement each other, and may be more efficient than an extensive survey of just one system.

27-04 Talk

POSITIVE SELECTION FACILITATES INTERSPECIFIC GENE TRANSFER IN HAWAIIAN ENDEMIC SCHIEDEA

Maxim V. Kapralov [1], Antonina A. Votintseva [1], Dmitry A. Filatov [1]

[1] *University of Birmingham, School of Biosciences, Edgbaston, B15 2TT, Birmingham, UK*

m.kapralov@bham.ac.uk

Rapid morphological and ecological changes during adaptive radiations on islands remain one of the most puzzling evolutionary phenomena. Interspecific hybridization may play a significant role during rapid adaptive radiations, as it allows adaptive mutations to spread across several species. To study the role of horizontal gene transfer during adaptive radiations we obtained partial sequences of 30 nuclear and 3 chloroplast protein coding genes from 27 species of Hawaiian endemic plant genus *Schiedea* (*Caryophyllaceae*), which represent a wide range of morphological forms (varying from vines to woody shrubs and perennial herbs) and occupy habitats from wet rainforest to dry desert-like conditions. According to our estimates, the silent divergence in nuclear genes between the species in the genus does not exceed 5%, suggesting that all the morphological and ecological diversity in this genus should have evolved fairly recently. Gene trees of three nuclear genes and of the chloroplast genes revealed deviations from the species tree, suggesting that the phylogenies of these genes have been distorted by horizontal gene transfer. Interestingly, positive selection was detected in all three nuclear and one of the chloroplast genes using maximum likelihood approach. The strongest topological conflict was found between species phylogeny and the chloroplast gene *rbcL*. Geographic distribution of *rbcL* hapoltypes suggests that positive selection might have caused the spread of advantageous *rbcL* haplotypes across several species co-occurring on the same islands. The presence of signal of positive selection in the nuclear and the chloroplast genes with distorted phylogenies supports the hypothesis that species may often share adaptive mutations during rapid adaptive radiations on islands.

27-05 Talk

A SELECTIVE SWEEP IN THE CHLOROPLAST DNA OF DIOECIOUS SILENE (SECTION ELISANTHE)

Graham Muir [1], Dmitry Filatov [1]

[1] *University of Birmingham, Biosciences, Edgbaston, B15 2TT, Birmingham, U.K.*

g.muir@bham.ac.uk

Gene flow occurs predominantly via pollen in angiosperms, leading to stronger population subdivision for maternally inherited markers, relative to paternally or biparentally inherited genes. In contrast to this trend, population subdivision within *Silene latifolia* and *S. dioica*, as well as subdivision between the two species is substantially lower in maternally inherited chloroplast genes, compared to paternally inherited Y-linked genes. A significant frequency spectrum bias towards rare polymorphisms and a significant loss of polymorphism in chloroplast genes compared to Y-linked and autosomal genes suggests that intra- and inter-specific subdivision in the chloroplast DNA may have been eroded by a recent selective sweep that has crossed the *S. latifolia* and *S. dioica* species boundary.

27-06 Talk

A CURIOUS COINCIDENCE: MOSQUITO BIODIVERSITY AND THE LIMITS OF THE JAPANESE ENCEPHALITIS VIRUS IN AUSTRALASIA

Stéphane Hemmerter [1], Jan Šlapeta [2], Nigel W. Beebe [1]

[1] *University of Technology, Sydney, Institute for the Biotechnology of Infectious Diseases, 1 Broadway, Ultimo, New South Wales, 2007, Sydney, Australia*
[2] *University of Sydney, Faculty of Veterinary Science, New South Wales, 2006, Sydney, Australia*

Stephane.Hemmerter@uts.edu.au

The mosquito *Culex annulirostris* Skuse (Diptera: Culicidae) is the major vector of endemic arboviruses in Australia and is also responsible for the establishment of the Japanese encephalitis virus (JEV) in southern Papua New Guinea (PNG). Regular JEV activity occurs on the islands separating PNG and Australia, yet JEV has not established on mainland Australia. We address the hypothesis that detailing the genetic diversity in *Cx. annulirostris* will shed light on the paradox that JEV can cycle just 70 km north of Australia yet not establish on mainland Australia. First we used the mitochondrial COI gene from mosquitoes collected throughout Australia and the southwest Pacific region to describe the biogeography of *Cx. annulirostris* using a hypothesis-testing phylogenetic framework. Then, we examined the extent of congruence between COI identified lineages and lineages identified using nuclear markers including the apyrase, acetylcholinesterase and olfactory receptor genes. Both Maximum Likelihood and Bayesian analyses reveal supporting evidence for several divergent geographically restricted lineages. Importantly, we were able to identify divergent COI lineages that coincide exactly with the current southern limit of JEV activity in Australasia. We discuss the outcomes of a multi-maker survey in describing the biogeography of *Culex* mosquitoes and suggest that COI is a reasonable starting point in understanding the evolutionary history of mosquitoes in this region. This information is also valuable in studying mosquito-borne disease in Australia and for the rational design of JEV vector competence experiments.

27-07 Talk

INCOMPLETE LINEAGE SORTING OR HYBRIDISATION? MULTILOCUS PHYLOGENY AND COALESCENT SIMULATION SUGGEST INTROGRESSIVE HYBRIDISATION IN ASEXUAL COMPLEX OF EUROPEAN LOACHES

Zuzana Musilova [1], Lukas Choleva [1], Alena Sediva [2], Karel Janko [2]

[1] *Charles University in Prague, Department of Zoology, Vinicna 7, 12844, Prague, Czech Republic*
[2] *Academy of Sciences of the Czech Republic, Institute of Animal Physiology and Genetics, Rumburska 89, 27721, Libechov, Czech Republic*

zuzmus@email.cz

The incomplete lineage sorting and hybridisation are both processes tending to produce incongruent phylogenetic signals obtained from different markers and resulting in discrepances between gene- and species trees. European loaches of the genus *Cobitis* are challenging group to study both phenomena as recent speciation events and hybridisation leading to asexuality have all been discovered there. We applied phylogenetic and phylogeographic analyses of mtDNA and several nuclear genes as well as AFLP markers to study the evolution of this group comprising three widespread species, *C. taenia, C. tanaitica* and *C. elongatoides*. Albeit *C. taenia* and *C. elongatoides* form well differentiated clades in all markers, *C. tanaitica* is a mosaic having mtDNA derived from *C. elongatoides*, while their nucleus appears to be closely related to *C. taenia*. Using Bayesian inference of contemporary and historical population sizes and speciation times, we have shown based on the supposed species-tree, that hybridisation is the most likely reason for the observed mtDNA gene-tree. All three species have parapatric ranges with restricted zones of overlap and, surprisingly enough, *C. tanaitica* is fully fixed for *elongatoides*-type mtDNA even in areas distant from *C. elongatoides*. The introgressive hybridisation is surprising in this group as all hybridisation events observed so far suggest either some undetected Mendelian hybridisation or evolution of sexual species via hybrid clones.

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27-08 Talk

DETERMINISM OF MITOCHONDRIAL GENETIC DIVERSITY IN BIRDS AND MAMMALS

Nabholz Benoit [1], Mauffrey Jean-François [2], Bazin Eric [3], Galtier Nicolas [1], Glemin Sylvain [1]

[1] *University Montpellier II, Institut des Sciences de l'Evolution, Place E. Bataillon, 34095, Montpellier - cedex 5, France*
[2] *Université de Provence-IRD, Laboratoire "Population-Environnement-Développement" UMRD151, 13331, Marseille cedex 3, France*
[3] *University of Reading, School of Biological Sciences, Reading RG6 6BX, Whiteknights,, UK*

bnabholz@univ-montp2.fr

Mitochondrial DNA (mtDNA) is one of the most popular population genetic markers. Its relevance as an indicator of population size and history has recently been questioned by several large-scale studies in animals : evidence for recurrent adaptive evolution was reported, at least in invertebrates (Bazin *et al.* 2006) and use mtDNA as only source of genetic marker seem to be problematic. Here we focus on more restricted taxonomic groups for which the issue of mtDNA near-neutrality and congruence with nuclear DNA patterns of variablity is crucial. By analysing the distribution of mtDNA diversity across ~140 mammalian and ~100 avian species, and relating it to allozyme diversity, census population size (available only for birds), life history traits, and taxonomy, we show that: (i) mtDNA in theses groups does not reject the nearly-neutral model; (ii) mtDNA diversity, however, is unrelated to life-history variables or population size; (iii) mtDNA diversity is highly variable between orders and families; (iv) this taxonomic effect is most likely explained by variations of mutation rate between lineages. The claim of a prominent role for adaptive evolution in animal mtDNA is therefore not supported for large vertebrate species but, surprisingly, even in these taxa population size is apparently not the prime determinant of mtDNA genetic diversity.

27-09 Talk

SPECIATION HISTORY OF WHITE-EYES (ZOSTEROPS [GRISEOTINCTUS]) COMPLEX IN THE SOLOMON ARCHIPELAGO: CONTRAST BETWEEN ANONYMOUS NUCLEAR LOCI AND MTDNA

Patricia H. Brito [1], Christopher E. Filardi [2], Robert G. Moyle [3], Scott V. Edwards [1]

[1] *Harvard University, Organismic and Evolutionary Biology, 26 Oxford Street, 02138, Cambridge, USA*
[2] *American Museum of Natural History, Center for Biodiversity and Conservation, Central Park West at 79th Street, 10024, New York, USA*
[3] *The University of Kansas, Ornithology, 1345 Jayhawk Boulevard, Dyche Hall, 66045, Lawrence, USA*

pbrito@oeb.harvard.edu

The Solomon Islands have been the stage for many classical hypotheses about avian biogeography and speciation, one being the paradox of the great speciators, as exemplified by the white-eyes (*Zosterops* [*griseotinctus*] species-complex). This paradox describes species whose dispersal ability was high enough to disperse populations to many islands, yet sufficiently low that differentiation could occur in each island. We used a multilocus approach employing anonymous loci to unravel the history of speciation and phylogenetic relationships in the white-eyes of the Solomon archipelago, focusing on the geography and timing of genetic differentiation, and estimation of population divergence times and ancestral population sizes. Whereas the anonymous loci exhibited substantial heterogeneity in gene trees, they were all consistent with an overarching pattern of differentiation at the level of species. These results are contrasted with results obtained from sequencing a mitochondrial coding gene, which exhibited strong phylogenetic signal delineating gene clades. We discuss the relative value of multilocus versus single approaches, highlighting the distinction between hypotheses addressed at the species versus the population levels.

27-10 Talk

WHEN MTDNA IS NOT ENOUGH: CONFLICTS AMONG MARKERS REVEAL MISLEADING MTDNA HISTORIES

Pierre-André Crochet [1], Julien Renoult [1], Alban Guillaumet [1], José Brito [2]

[1] *UMR5175 CEFE, 1919 route de Mende, 34293, Montpellier cedex 5, France*
[2] *CIBIO / UP, R. Padre Armando Quintas, 4485-661, Vairão, Portugal*

pierre-andre.crochet@cefe.cnrs.fr

Mitochondrial DNA is the most widely used marker to infer population history. However, several phenomena can create mismatch between mtDNA history and population history, including random lineage sorting and gene flow. In large gulls, we showed that a mixture of incomplete lineage sorting and hybridisation maintains mtDNA lineage sharing among virtually all current species. In the Iberian Wall Lizards, we found that past introgression resulted in polymorphism for mtDNA lineage in one taxon and extensive replacement of original mtDNA by alien mtDNA in another taxon. In the *Galerida* larks, lineage sharing was found to be much less frequent but occurred in all three species. On the contrary, we did not detect any mtDNA mismatch in the *Iberolacerta* lizards. In conclusion, three of the four groups that we have investigated showed examples of misleading mtDNA relationships. In other cases originating from our own research (*Acanthodactylus* lizards) or from the literature (for example the green toad *Bufo viridis*), mtDNA mismatch was not demonstrated but deep mitochondrial divergences are found between populations that seem undistinguishable based on ecology and morphology. We suggest that coalescence processes rather than cryptic biological diversity are a possible explanation for such cases of unexpected mtDNA diversity. In conclusion, current projects to characterise biodiversity from mtDNA diversity only (DNA barcoding) are likely to be misleading especially where they are most needed i.e. among closely related species. We argue that DNA barcoding should be based on the use of multiple loci.

27-01 Poster

WHY DOES GENETIC DIVERSITY OF MITOCHONDRIAL GENES NOT REFLECT POPULATION SIZE?

Emily Knott [1]

[1] *University of Jyväskylä, Biological & Environmental Sciences, P.O. Box 35, 40014, University of Jyväskylä, Finland*

kknott@cc.jyu.fi

Bazin and colleagues recently reported (Science 312:570-572) that mitochondrial DNA diversity is not correlated with either nuclear DNA diversity or allozymic heterozygosity. This finding emphasizes important questions about the suitability of mitochondrial DNA as a neutral marker, and the authors propose that recurrent adaptive evolution in the mitochondrial genome has led to the observed pattern. Here, I examine diversity of mitochondrial genes from echinoderms and molluscs in more detail, specifically focusing on the effects of population differentiation on genetic diversity estimates. Since differentiation among populations is likely first observed in the mitochondrial genome, population level variation in nucleotide frequencies may artificially inflate diversity estimates when the data are combined.

27-02 Poster

LONG-RANGE DISPERSAL AND THE FATE OF A MUTATION ARISING IN THE COLONIZATION FRONT

Julien Fayard [1], Etienne K. Klein [1, 2], François Lefèvre [1]

[1] *INRA Avignon, UR 629, Recherches Forestières Mediterranéennes, Domaine St Paul, Site Agroparc, 84914 Avignon, France*
[2] *INRA Avignon, UR 546, Biostatistique et Processus Spatiaux, Domaine St Paul, Site Agroparc, 84914 Avignon, France*

julien.fayard@avignon.inra.fr

Colonization is a key process affecting both the dynamics of population expansion and the spatial structure of diversity. Interaction between both processes is illustrated by the fate of a neutral mutation arising in the colonization front under a stepping-stone model. It can “surf” with the front wave and reach a higher frequency and a wider spatial distribution than expected in stationary populations (Edmonds et al. 2005).

Long-distance dispersal has contrasted effects on diversity, both increasing the founder effects and leading to more diverse propagules pools at long-distances. We thus extended the model from Edmonds et al. 2005 (simulation on a rectangular lattice of demes with stochastic demography and dispersal) to account for long distance dispersal. We investigated (i) how the behaviour of the neutral mutation arising in the colonization front is modified by the long distance dispersal, (ii) the impact of the size of the colonized corridor and (iii) the impact of the fine spatial distribution of non-mutants locally around the place where mutation occurred.

We demonstrated that long distance dispersal can prevent the surfing phenomenon only if the width of the simulation domain is large. Oppositely, when the width of the domain becomes smaller, the neutral mutation arising in the colonization front more often surfs with the front, whatever the kind of dispersal kernel. We also demonstrated that non-mutants competing with mutants (either locally or globally) during the early stages of the simulation affect the fate of the neutral mutation arising in the colonization front. Finally, no impact of the degree of fragmentation of the colonization front in which the mutation arises was found.

27-03 Poster

APPROXIMATE BAYESIAN COMPUTATION - CENTRAL QUESTIONS & SOME ANSWERS

Joao S. Lopes [1]

[1] *University of Reading, School of Biological Science, 4th floor Lyle Building, University of Reading, RG6 6AJ, Reading, United Kingdom*

joao.lopes@rdg.ac.uk

Approximate Bayesian Computation (ABC) is a recent developed Bayesian technique that can be used to extract information from DNA data. This method has been firstly introduced to Population Genetics in 1999 by Pritchard. It relies in two major approximations: the use of a simulated step that substitutes the necessity of using an explicitly likelihood function; and the summarization of DNA data with a set of summary statistics.

This Bayesian approach can be used to estimate several demographic history parameters, from populations, using DNA data. Its main advantages are the decrease on computation time demanding and the increase on efficiency and flexibility when dealing with multiparameter models.

A particular ABC method, similar to the one used by Mark Beaumont in 2006, is being studied against a commonly used Markov Chain Monte Carlo (MCMC) method (Hey and Nielsen, 2004) to infer the accuracy of the previous. These approaches use DNA sequence data to extract demographic information (e.g. population sizes, time of splitting events, migration rates) within a two populations "Isolation with Migration" model. It has been also explored the use of ABC with a more complex demographic model.

In a recent approach the developed ABC method has been tested within several different conditions. These conditions comprise the use of different summary statistics sets; different number of iterations; different tolerance intervals and the use or not of the regression step introduced by Beaumont and co-authors in 2002.

Finally the ABC framework was applied to a published data set firstly study with an MCMC method (Won & Hey, 2005).

These studies confirm the competitiveness of the recently explored Bayesian method when compared to a standard MCMC approach. Its potential role on researches with more complex, therefore more realistic, models is emphasized.

27-04 Poster

EVIDENCE FOR INTERSPECIFIC GENE FLOW FROM BROAD SCALE PATTERNS OF GENETIC AND GEOGRAPHIC DISTANCES

Jeannette Whitton [1], John F. Bain [2], Michael C. Whitlock [3]

[1] *University of British Columbia, Botany, 3529-6270 University Boulevard*
, V6T 1Z4, Vancouver, British Columbia, Canada
[2] *University of Lethbridge, Biological Sciences, 4401 University Drive, T1K 3M4, Lethbridge, Alberta, Canada*
[3] *University of British Columbia, Zoology, 6270 University Boulevard, V6T 1Z4, Vancouver, British Columbia, Canada*

jwhitton@interchange.ubc.ca

Studies of hybridization in a range of plant taxa reveal the complex and diverse outcomes of hybridization, including localized and limited gene flow, broad scale introgression, homoploid and polyploid hybrid speciation. The frequency of each of outcomes has been thought of as a function of the strength of reproductive isolation between taxa, which will affect the frequency of hybrid formation and the fitness of hybrids and introgressants. Here we examine geographical patterns of gene flow using an approach based on a modified Mantel's test, based on only inter-taxon genetic and geographic distances. The data employed are from a range of marker types and taxa, sampling broadly across the geographic range of the taxa. Some of the pairs of taxa (e.g. Lasthenia) have overlapping ranges and were previously known to hybridize. In other cases (Townsendia), taxa are allopatric and interspecific gene flow had not been reported. We were able to detect evidence for geographical structuring of genetic distances in a number of inter-taxon comparisons, including some previously unsuspected cases of hybridization. We outline the method and its assumptions and explore other possible interpretations, and conclude that the results suggest that unsuspected cases of introgression may be common in plant taxa.

27-05 Poster

GENE FLOW BETWEEN SILENE LATIFOLIA AND S. DIOICA: "POROUS" SPECIES BOUNDARY OR SHARED ANCESTRY?

Andrea L. Harper [1], Graham Muir [1], Dmitry A. Filatov [1]

[1] *University of Birmingham, Biosciences, Edgbaston, B15 2TT, Birmingham, UK*

alh571@bham.ac.uk

Silene latifolia (white campion) and *Silene dioica* (red campion) are two closely related dioecious species and their ranges broadly overlap across Europe. In geographic areas where the two species coexist, hybridization may occur, leading to gene flow between these two phenotypically distinct species. Previously it was demonstrated that Y-linked genes show very high Fst (~0.9) between the two species in contrast to the X-linked genes, which show moderate differentiation (Fst~0.3) between *S. latifolia* and *S. dioica*. This suggests that interspecific introgression of the Y chromosome is prevented by selection. Alternatively it may be the X-linked genes that are unusual in their ability to cross the species boundary. To establish the genome-wide rate of gene flow between the two species, we studied DNA diversity in 19 autosomal loci in a sample of 15 individuals from each species. Autosomal loci show less differentiation between the species (average Fst=0.39), compared to the Y chromosome. However, there is little evidence of significant historical gene flow between the two species and all the shared polymorphisms can be explained by the shared ancestral polymorphism. High Fst on the Y is likely to be due to reduced intraspecific polymorphism, which results in Fst value. Although hybridization between the two species clearly occurs, it might be a recent phenomenon and until recently *S. latifolia* and *S. dioica* might have been isolated by geographic and/or ecological barriers.

27-06 Poster

MULTIPLE ORIGINS OR INTROGRESSION – POLYPLOID SPECIATION IN CAPSELLA (BRASSICACEAE)

Tanja Slotte [1], Alf Ceplitis [2], Huirun Huang [3], Martin Lascoux [1]

[1] *Uppsala University, Department of Evolution, Genomics and Systematics, Norbyv. 18D, 75236, Uppsala, Sweden*
[2] *Lund University, Department of Cell and Organism Biology, Solveg. 29, 22362, Lund, Sweden*
[3] *Chinese Academy of Sciences, South China Botanical Garden, Leyiju, Guangzhou, Guangdong 510650, China*

Tanja.Slotte@ebc.uu.se

Polyploidization, often accompanied by hybridization, has been a major force in flowering plant evolution. Polyploid speciation is often regarded as a special form of instantaneous speciation, where reproductive isolation arises immediately. Hence, patterns of shared polymorphism across ploidy levels have been taken as evidence for multiple origins. However, triploid plant hybrids are often semi-fertile, and allele sharing could therefore also be explained by hybridization and introgression. Here, we assess these competing hypotheses in the genus *Capsella* (Brassicaceae), using DNA sequence data from six independent nuclear low-copy genes. We find that the tetraploid *C. bursa-pastoris* shares alleles with the diploid *C. rubella* in western Eurasia, where the two species occur in partial sympatry. In eastern Eurasia, where *C. bursa-pastoris* is allopatric to *C. rubella*, no allele sharing was found. This type of pattern is often taken as a hallmark of introgression. We then assess gene flow between *C. bursa-pastoris* and *C. rubella* in both regions, using an isolation-with-migration model. These analyses indicate that there has been unidirectional gene flow from *C. rubella* to *C. bursa-pastoris* in western Eurasia. No gene flow was inferred in eastern Eurasia. Estimates of the timing and extent of introgression suggest that a few introgression events during or after the last glaciation are sufficient to explain present-day patterns of variation in *C. bursa-pastoris*. Our findings show that allele sharing across ploidy levels need not be due to multiple origins of the polyploid, but can be caused by post-polyploidization hybridization and introgression, and provide a clear demonstration of the need to explicitly address both alternative hypotheses.

27-07 Poster

POPULATION DIFFERENTIATION AND SPECIES COHESION IN PLANT SPECIES ADAPTED TO NEOTROPICAL HIGH-ALTITUDE 'INSELBERGS'

Thelma Barbará [1], Gustavo Martinelli [2], Michael F. Fay [1], Simon J. Mayo [3], Christian Lexer [1]

[1] *Royal Botanic Gardens Kew, Jodrell Laboratory, TW9 3DS, Richmond, Surrey, United Kingdom*
[2] *Jardim Botânico do Rio de Janeiro, Instituto de Pesquisas, Rua Pacheco Leão 915, 22460-030, Rio de Janeiro, Brazil*
[3] *Royal Botanic Gardens Kew, Herbarium, TW9 3AB, Richmond, Surrey, United Kingdom*

thelmabarbara@btinternet.com

Isolated granitic rock outcrops or 'inselbergs' may provide a window into the molecular ecology and genetics of continental radiations under simplified conditions, in analogy to the use of oceanic islands in studies of species radiations. We aimed at using plastid and nuclear DNA markers to study population differentiation and gene flow in two diploid, perennial plants adapted to high-altitude neotropical inselbergs, *Alcantarea imperialis* and *A. geniculata* (Bromeliaceae). Plastid DNA regions known to be variable in many monocot groups turned out to be of little help in *Alcantarea* due to low levels of variability, which mirrors molecular phylogenetic studies indicating slow evolutionary rates of plastid DNA in Bromeliaceae. Population differentiation for nuclear microsatellites is pronounced in both taxa, especially in *A. imperialis*. Nuclear marker-based estimates of gene flow in this species are considerably lower than expected from the literature on plants in general and Bromeliaceae in particular, and too low to prevent differentiation due to drift ($N_em < 1$), unless selection coefficients/effect sizes of favorable alleles are great enough to maintain species cohesion. Population subdivision in one inselberg population of *A. imperialis* appears to be associated with the presence of two color morphs that differ in the coloration of rosettes and bracts. Our results indicate a high potential for inselbergs as venues for studies of the molecular ecology and genetics of continental radiations. These insights would not have been possible based on a single-locus survey of plastid DNA alone.

27-08 Poster

CONFLICTING MITOCHONDRIAL AND NUCLEAR DATA IN THE SIX TOOTHED SPRUCE BARK BEETLE

Wolfgang Arthofer [1], Dimitrios N. Avtzis [1], Christian Stauffer [1]

[1] *University of Natural Resources and Applied Life Sciences, Institute of Forest Entomology, Forest Pathology and Forest Protection, Hasenauerstrasse 38, 1190, Vienna, Austria*

wolfgang.arthofer@boku.ac.at

The six toothed bark beetle, *Pityogenes chalcographus* (Coleoptera, Scolytinae) is a major pest in European spruce stands. Analysis of about 10% of the mitochondrial DNA revealed a maximum sequence divergence of 2.3% and the sympatric coexistance of two genetically distinct groups, a pattern mostly observed in populations that initially evolved in allopatry and afterwards came in secondary contact. These findings are consistant with crossing barriers observed by E. Führer in the 1970ies and with the hypothesis that during Quaternary glaciations *P. chalcographus*, like its host tree, was restricted to at least three separated refugial areas.

To further elucidate the beetle's population structure we analyzed four highly polymorphic nuclear microsatellite loci, a 860 bp part of the 28S rDNA gene and a 1 kbp fragment of the Elongation Factor 1α gene. Other than mitochondrial DNA all nuclear markers show low levels of gentic diversity across Europe. These results are indicative for unequal male and female genealogies. We discuss sex biased dispersal rates, repeated bottleneck effects due to outbreak associated fluctuations in population size and the presence of the reproductive manipulating endosymbiont *Wolbachia* as potential factors shaping the incongruent history of the beetle's nuclear and mitochondrial genome.

27-09 Poster

TEMPORAL CHANGES IN THE POPULATION STRUCTURE OF AN INVASIVE SPECIES IN EUROPE

Alessandro Grapputo [1, 2], Sanna Boman [2], Leena Lindström [2], Anne Lyytinen [2], Johanna Mappes [2]

[1] *Univ. of Padova, Dept. of Biology, Via U. Bassi 58/B, 35121, Padova, Italy*
[2] *Univ. of Jyväskylä, Dept of Biological & Environ. Sciences, Survontie, 9, 40014, Jyväskylä, Finland*

grapputo@bio.unipd.it

The evolutionary history of invasive species typically involves complex changes in effective population size with strong founder effects during colonization events followed by rapid expansions. The rate and extent of invasive fronts may depend on the amount and pattern of gene flow among populations of invasive species and the knowledge of their dispersal mode and population structure gives valuable information to improve their management strategies. The Colorado potato beetle is an invasive species which invaded Europe at the begging of the last century. A single invasion seems to have took place with a relative strong founder effect (Grapputo et al. 2005) followed by a rapid expansion and colonization of almost all Europe. In this work we analysed, using ALFP markers, the temporal changes in the population structure of the populations forming the most north-eastern front of the beetle expansion in Europe and their effective population sizes.

27-10 Poster

THE EFFECTS OF POST-GLACIAL HISTORY AND ISOLATION ON NORTHERN RANGE MARGIN POPULATIONS OF THE BUTTERFLY COENONYMPHA ARCANIA

Anna Cassel-Lundhagen [1], Thomas Schmitt [2], Niklas Wahlberg [3], Jack Windig [4], Sören Nylin [5], Nils Ryrholm [6], Toomas Tammaru [7]

[1] *SLU, Ecology, Box 7044, 75007, Uppsala, Sweden*
[2] *University of Trier, Biogeography, Am Wissenschaftspark 25-27, 54296, Trier, Germany*
[3] *University of Turku, Biology, 20014, Turku, Finland*
[4] *Animal Sciences Group, Edelhertweg 15, 8200 AB, Lelystad, Netherlands*
[5] *Stockholm University, Zoology, 10691, Stockholm, Sweden*
[6] *Gävle University, Kungsbäcksvägen 47, 80176, Gävle, Sweden*
[7] *University of Tartu, Zoology and Hydrobiology, Vanemuise 46, EE-51014, Tartu, Estonia*

anna.lundhagen@ekol.slu.se

Populations at range margins with different degree of isolation provide an opportunity to study the relative microevolutionary role of historical events, gene flow and selective pressures. This project studied the effects of evolutionary processes in pearly heath butterfly populations by combining data obtained from neutral genetic markers and traits subjected to selection. Butterflies from three regions were analysed representing central (Ce), marginal but connected (MCo) as well as marginal and isolated parts (MI) of the species distribution. The number of mtDNA haplotypes did not differ between the MC and MI populations, although the predominating haplotype were different implying different postglacial colonisation origins. Allozyme variability, on the other hand, was significantly lower in MI populations compared to the other regions. Level of variability did not differ between MC and central populations. Butterflies from the MI region had significantly smaller wings than individuals from the MCo and Ce regions and differed in wing pattern characteristics. These results show that isolation can create opportunities for rapid neutral and non-neutral genetic differentiation through drift and selection that may eventually lead to speciation. These processes seem to be significantly counteracted in the marginal but connected populations by gene flow from more central areas.

27-11 Poster

POPULATION HISTORY OF NASONIA VITRIPENNIS

Bernd Grillenberger [1], Louis Van de Zande [1], Kuke Bijlsma [1], Juergen Gadau [2], Leo W. Beukeboom [3]

[1] University of Groningen, Evolutionary Genetics, PO Box 14, 9750AA, Haren, The Netherlands
[2] Arizona State University, School of Life Sciences, PO Box 14, 9750AA, Tempe, AZ, USA
[3] University of Groningen, Evolutionary Genetics, PO Box 874501, 85287-4501, Haren, The Netherlands

b.grillenberger@rug.nl

Mitochondrial and nuclear markers are widely used in phylogenetic analzsis, but not always with equal outcome. The parasitic wasps from the genus *Nasonia* are thought to have evolved in North America. In *Nasonia* there are three species known. *N. vitripennis* which is cosmopolitan, *N. giraulti* which occurs in eastern North America, and *N. longicornis* which occurs in western North America only. *N. vitripennis* is thought to be the ancestral species in this genus. We analyzed a 399 bp fragment of the mitochondrial Cytochrome Oxidase I gene of 89 *N. vitripennis* specimen from European and North American populations. We found a seven times higher genetic variation among the European samples compared to North America. A screen of nine polymorphic microsatellites on the same samples showed no difference in genetic variation between North America and Europe. These contradictive results allow two interpretations: (1) The North American population went through a severe bottleneck and lost most of its genetic variation. This event is not visible in the microsatellite data due to the high mutation rate of this marker. (2) The North American population experienced a selective sweep of a beneficial mitochondrial haplotype and therefore kept its nuclear variation. The pros and cons of the two hypotheses are discussed.

27-12 Poster

THE EVOLUTION OF SOUND PRODUCTION MECHANISMS IN THE GENUS SPHINGONOTUS FIEBER, 1852

Martin Husemann [1], Jana Deppermann [1], Axel Hochkirch [1]

[1] University of Osnabrück, Department of Biology/Chemistry, Barbarastr. 13, D-49076, Osnabrück, Germany

hochkirch@biologie.uni-osnabrueck.de

The genus *Sphingonotus* is one of the largest grasshopper genera, containing more than 100 species, which occur throughout the Mediterranean, Central Asia and East Asia. Most of the species are confined to semi-desert or desert habitats. Four different mechanisms of song production are known within the genus *Sphingonotus*, three of which include veins of the fore wing, such as a serrate intercalary vein, a serrate radial vein or knots between Media and Radia. Another mechanism of sound production is wing crepitation, which is produced by stiffened anal veins of the hind wing. We used sequences of two mitochondrial genes (ND5, ND1) and a nuclear gene (ITS2) to infer a phylogenetic hypothesis for the genus *Sphingonotus* and its allies. Our results show that the genera *Sphingonotus, Pseudosphingonotus* and *Wernerella* are polyphyletic and two recent radiations exist which contain a high number of species (*S. caerulans*- and *P. azurescens*-group). While the serrate intercalary vein is the plesiomorphous type of sound production, the knots between Media and Radia are only found in one lineage. However, in one species (*P. savignyi*) both mechanisms can be found - sometimes even in one specimen. Wing crepitation occurs in different lineages of the genus and evolves independently from the mechanisms on the fore wings. Two species (*S. rubescens*, *S. caerulans*) are difficult to distinguish with molecular markers, but produce species-specific sounds. Currently, we use AFLP to obtain a better resolution of the young radiations.

27-13 Poster

A MULTILOCUS APPROACH TO THE MOLECULAR SYSTEMATICS OF THE D. VIRILIS GROUP OF SPECIES

Ramiro Morales-Hojas [1], Cristina P. Vieira [1], Jorge Vieira [1]

[1] *IBMC, Molecular Evolution Lab, Rua do Campo Alegre 823, 4150-180, Porto, Portugal*

rmhojas@ibmc.up.pt

We have used a multilocus approach using four nuclear genes and the 16S-12S mtDNA to reconstruct the phylogeny of the Drosophila virilis group of species. The ages of the species have been also estimated using r8s and multidivtime assuming a relaxed molecular clock. Major cladogenesis events correlate with geological and palaeoclimatic events, and an evolutionary history is proposed based on these. The phylogenetic relationships of the major clades was not resolved and it is proposed, based on the ages of the nodes, that it is the consequence of fast successive cladogenesis events (hard polytomy). Furthermore, the systematics of D. americana americana, D. a. texana and D. novamexicana is investigated in more detail using 12 nuclear genes from several strains for each taxa. The phylogeny of the 12 genes combined result in the reciprocal monophyly of D. americana and D. novamexicana, and there is significant genetic differentiation between them at all genes. However, D. a. americana (X/4 fusion form) and D. a. texana (non fusion form) show no reciprocal monophyly in the phylogeny and even more, there is no genetic differentiation between the two chromosomal forms with the exception of those genes located nearby the chromosomal rearrangements that differentiate them. The estimated ages of divergence for D. novamexicana and D. americana are concordant with previous estimates. The restricted geographical location of D. novamexicana to the western slopes of the Rocky mountains suggests that D. novamexicana evolved from a marginal, peripheral population of the D. americana/D. novamexicana ancestral species. Furthermore, the mid- to late-Pleistocene is a period characterised by pluvial-interpluvial cycles in Southwest North America that may have influenced the evolution and diversification of these species.

27-14 Poster

EVIDENCE FOR WIDESPREAD HETEROPLASMY AND RECOMBINATION OF MTDNA IN DROSOPHILA MELANOGASTER

Maria D. S. Nunes [1], Christian Schlötterer [1, 2]

[1] *University of Veterinary Medicine Vienna, Institute of Animal Breeding and Genetics, Josef Baumann Gasse 1, 1210, Vienna, Austria*
[2] *University of Innsbruck, Institute of Ecology, Technikerstr. 25, A-6020, Innsbruck, Austria*

daniela.nunes@i122server.vu-wien.ac.at

Strict maternal inheritance and absence of recombination was considered a hallmark of animal mtDNA. Despite some recent reports of heteroplasmy and recombination the evidence is still controversial. Here we provide for the first time evidence that paternal leakage leads to heteroplasmy and recombination in natural *D. melanogaster* populations. Using a highly sensitive quantitative real-time PCR (qrt-PCR) assay, we show that at least 8% of the individuals carry different mitochondrial haplotypes that originated from paternal leakage. Sequence analysis of COI and ND4 fragments in 61 individuals resulted in two incompatible genealogies, which strongly suggests recombination in *D. melanogaster* mtDNA.

27-15 Poster

OLFACTORY AND GUSTATORY RECEPTOR GENE EXPRESSION IN DROSOPHILA: TOWARDS DETERMINING THE ROLE OF CHEMOSENSORY GENES IN SPECIATION

Johanna F. Nielsen [1], Anastasia Gardiner [2], Mike G. Ritchie [2], Roger K. Butlin [3], William C. Jordan [1]

[1] *Zoological Society of London, Institute of Zoology, Regent's Park, NW1 4RY, London, United Kingdom*
[2] *The University of St. Andrews, School of Bioloy, St. Andrews, KY16 9TH, Fife, United kingdom*
[3] *The University of Sheffield, Animal and Plant Sciences, Western Bank, S10 2TN, Sheffield, United Kingdom*

johanna.nielsen@ioz.ac.uk

Chemoreception describes the process of sensing chemical signals and thus forms a major part of the interaction between an organism and its environment. In *Drosophila*, airborne chemicals are detected by Olfactory Receptors (OR) whereas non-volatile signals are detected by Gustatory Receptors (GR). As both olfactory and gustatory signals play a major role in habitat and mate choice, two processes which generate prezygotic reproductive isolation, OR and GR genes are likely to play key roles in the speciation process. Although genome sequencing has identified coding sequence differences between several *Drosophila* species, any differences in gene expression of these loci among species remain unknown. In order to gain further knowledge on the changes in functional divergence of OR and GR loci, and thus the evolution of prezygotic isolation, it is important to determine to what extent changes in gene expression vs. coding sequence evolution plays. This study investigates relative gene expression differences of OR and GRs on the 3R chromosome in six *Drosophila* species and utilises real-time PCR to generate both presence/absence and relative expression data. In conjunction with genome sequence data (Gardiner et al., in prep) it will then be used to investigate any correlations between coding sequence and gene expression divergence. This combined data has the potential to determine the relative roles of structural and expression modifications in generating prezygotic reproductive isolation and to identify which OR and GRs play key roles as candidate “speciation genes”.

27-16 Poster

INTER- AND INTRA-SPECIES VARIATION AT HOMING ENDONUCLEASE RECOGNITION SITES IN MALARIA VECTORS; IMPLICATIONS FOR MALARIA CONTROL.

Samantha M. O'Loughlin [1], Austin Burt [1]

[1] *Imperial College, NERC Centre for Population Biology, Silwood Park, SL5 7PY, UK*

s.oloughlin@imperial.ac.uk

Genetic modification of wild *Anopheles* populations to arrest the spread of malaria would be greatly expedited by the use of a driving mechanism, so that the genetic construct would be inherited at a high level and to overcome negative selective pressures. Homing endonucleases (HEGs) are selfish DNA elements that have the potential to act as driving mechanisms. HEGs occur in nature and recognise specific DNA sequences of about 25 bp as insertion sites. Ensembl searches have found HEG recognition sites in several important genes in *Anopheles gambiae*, one of the main malaria vectors in Africa. *An. gambiae* is a member of a complex of closely related species (the *Anopheles gambiae* complex) some of which are also important vectors, and which may hybridise in nature. We have sequenced the HEG recognition sites in *An. gambiae* species to determine inter- and intra- species variation, and will discuss the implications of variation for genetic control strategies.

27-17 Poster

INCONGRUENCE OF PHYLOGENETIC SIGNALS AND SHARED POLYMORPHISMS PREVENT THE MOLECULAR CHARACTERISATION OF THE CERATITIS FASCIVENTRIS, C. ANONAE, C. ROSA COMPLEX (DIPTERA: TEPHRITIDAE)

Massimiliano Virgilio [1], Thierry Backeljau [2], Marc De Meyer [1]

[1] *Royal Museum for Central Africa, Leuvensesteenweg 13, 3080, Tervuren, Belgium*
[2] *Royal Belgian Institute of Natural Sciences, Vautierstraat 29, 1000, Brussels, Belgium*

m.virgilio@unibo.it

Ceratitis fasciventris, C. anonae and C. rosa form a complex (hereafter referred to as FAR complex) of polyphagous pest species that are widespread in Africa. The present study investigates the genetic structuring of the FAR complex in order to assess whether a) the three morphospecies represent phylogenetically distinct groups and b) previous phylogenetic hypotheses on the complex are supported when specimens from a wider geographic sampling are considered. Fifty-six specimens of the three morphospecies from all over the distributional area of the complex were surveyed. Sequences of nuclear (Period) and mitochondrial markers (COI, ND6) were analysed for each specimen. The number of haplotypes at the different markers varied from 16 (Period) to 37 (COI). The three gene fragments yielded haplotypes that were shared among species. Surprisingly, maximum likelihood trees did not recover monophyletic groups corresponding to the three morphospecies. ND6 and COI divided C. fasciventris in two consistent and bootstrap supported clades, involving the specimens from Benin and from Mali/Ivory Coast, while the C. fasciventris specimens from Uganda and Kenya were mixed with the specimens of the two other species in a large, unresolved clade. In contrast, the Period gene was unable to recover the two C. fasciventris clades distinguished by COI and ND6. Hence, phylogenetic relationships among the three morphospecies appear far more complex than previously hypothesised, with incongruent signals a) among molecular markers and b) between molecular markers and morphological characters. Overall, these results did not support the monophyly of the three morphospecies but suggested that C. fasciventris is in itself a complex of cryptic taxa.

27-18 Poster

NUCLEAR AND MITOCHONDRIAL INSIGHTS INTO THE POPULATION STRUCTURE OF ATLANTIC SEABASS (DICENTRARCHUS LABRAX)

Ilaria Coscia [1], Katja Peijnenburg [1], Mike Pawson [2], Stefano Mariani [2]

[1] *Univeristy College Dublin, School of Biology & Environmental Science, UCD Campus - Science Centre (West), Belfield, D4, Dublin, Ireland*
[2] *CEFAS, Pakefield Road, NR33 0HT, Lowestoft, Suffolk, U.K.*

ilaria.coscia@ucd.ie

The seabass (*Dicentrarchus labrax*) has long represented a very valuable fisheries and aquaculture resource in the Mediterranean, but over the last decades its populations are increasing in the Atlantic coastal waters throughout north western Europe. Apart from a definite differentiation between Atlantic vs Mediterranean stocks, authors have not yet agreed on a finer scale stock structure identification for the purpose of management, and there still remain a high degree of uncertainty as to the processes underlying the current phase of demographic expansion of extant Atlantic populations. Here we have compared populations around Britain and Ireland (North Sea, English Channel, Irish Sea, Celtic Sea), as well as more southern samples (Bay of Biscay, Western Mediterranean), using a suite of 11 unlinked polymorphic microsatellites and a 434-bp fragment of mtDNA comprising part of the D-Loop. With the use of several statistical approaches, we attempt to disentagle present-day migration phenomena from historical colonisation events, and try to make use of the integrated multi-marker information to assess and describe the stock structure of the species.

27-19 Poster

EVOLUTIONARY PROCESSES IN MARINE PELAGIC FISHES: COMPARATIVE ANALYSES OF POPULATION STRUCTURE IN BIGEYE TUNA AND EUROPEAN SARDINE

Elena G. Gonzalez [1], Peter Beerli [2], Rafael Zardoya [1]

[1] *Museo Nacional de Ciencias Naturales, CSIC, Departamento de Biodiversidad y Biología Evolutiva, José Gutiérrez Abascal, 2, 28006 Madrid, Spain*
[2] *Florida State University, School of Computational Science (SCS) and Biological Sciences Department, Tallahassee, FL, US*

mcngj584@mncn.csic.es

Study of genetic variation patterns in marine pelagic fishes has proven to be a challenging task. Marine pelagic fishes show great dispersal capability, migratory movements, wide distributions, and large population sizes. These characteristics together with the apparent lack of significant physical barriers to dispersal in the marine realm are thought to lead to panmictic populations. However other life history traits (such as e.g. philopatric behaviour) and historical processes (e.g. past sea level and temperature fluctuations during the Pleistocene) may result in significant population genetic structure. In order to disentangle the relative role of life history traits and historical processes in shaping contemporary population genetics patterns of marine pelagic fishes the use of multiple (mitochondrial and nuclear) loci and the application of coalescent-based approaches is required. In this study, we use mitochondrial control region and microsatellite data to analyze population genetic structure of bigeye tuna (*Thunnus obesus*) and European sardine (*Sardina pilchardus*). For big eye tuna populations, we found very low genetic differentiation in between-oceans at nuclear level, in contrast with the significant genetic divergence between Atlantic and Indo-Pacific Oceans reported in mtDNA sequences. These pattern suggest homing behavior for Bigeye tuna and that interoceanic movements are more common among males than among females. In the case of sardine populations, the significant genetic structuring detected by mitochondrial data is reflecting past isolation due to temperature fluctuations during Pleistocene whereas microsatellite data revealed the existence of a present day panmictic population which follows an isolation-by-distance pattern.

27-20 Poster

STOCK STRUCTURE OF THE SWORDFISH, XIPHIAS GLADIUS, IN THE WESTERN INDIAN OCEAN: IMPORTANCE OF CONGRUENCE OF MARKERS IN A WAY OF STOCK ASSESSMENT.

Delphine Muths [1], Jérôme Bourjea [1], Claire Jean [1], Henri Grizel [1]

[1] *IFREMER Réunion, 97822, Le Port, France*

muths@sb-roscoff.fr

The swordfish *Xiphias gladius* is a highly migratory pelagic species heavily exploited by commercial fishery worldwide, mainly by longline fisheries. Despite a constant increase of fishery effort, captures of swordfish tend to decrease since 2000 in the South Western Indian Ocean and there is a strong suspicion of overfishing. Whether current assessment models are performed for managers, uncertainties remain considerable, even regarding biology and behaviour. So, in the aim of performing stronger stock assessment, we need to improve our knowledge on the genetic swordfish stock structure.In a first time, Jean *et al.* (2006)'s study failed to show population differentiation on the basis of microsatellite data in the South Western Indian Ocean in agreement with what could be suspected for a species displaying a high capacity of migration. On the opposite, Lu *et al.* (2006) showed with mitochondrial data obtained in the same geographic area that gene flow between adjacent populations appeared to be quite reduced or even absent. As these differences in conclusions can have important impact on stock assessment, it appears important to determine if they are due to sampling area, to sampling size or to markers discordance. That's why a microsatellite analysis (8 loci) combined to a mitochondrial control region haplotype analysis (540-bp sequences) was conducted on a total of 351 samples from six different sites of the South Western Indian Ocean. This step appeared to be necessary to be sure of the congruence of the evolutionary histories based on the two genetic markers for this species, for then conduct a genetic study at a global scale, *i.e.* the Indian Ocean and its connections with the neighbouring oceanic basins.

27-21 Poster

UNEXPECTED DIFFERENTIATION PATTERNS USING MTDNA AND ALLOZYMES IN TWO BRITTLE-STAR SPECIES: WHEN (DIS)SIMILARITIES ARE NOT THOSE EXPECTED TO BE…

Delphine Muths [1], Dominique Davoult [1], Didier Jollivet [1]

[1] *SBR, 29682, Roscoff, France*

muths@sb-roscoff.fr

The genetic structure of two brittle-stars, *A. brachiata* and *O. fragilis*, has been studied in the North-East Atlantic using allozymes and mtDNA. These genetic markers were chosen to better delineate the relative parts of population history and contemporary gene flow in shaping the present structure of both species. The two species display contrasted dispersal and colonisation potential (length of larval phase, habitat fragmentation), which led to expect differences in genetic pattern (*i.e.* isolation-by-distance *versus* n-island model). Unexpectedly, these species displayed a high level of similarity in population structure for both markers but contrasted findings between markers. Both species presented within-species deep divergent lineages. Within lineages, they both showed no differentiation on the basis of the mtDNA but strong genetic differences between nearly all populations when using allozymes. Genetic discrepancies obtained between the two markers within each species may be explained by various evolutionary rates between markers but also by the way how polymorphisms were treated. The absence of differentiation with mtDNA is indeed in agreement with the recent expansion phase of species since the opening of the English Channel. Conversely, the high level of "chaotic" genetic differentiation observed with allozymes may be explained by a great level of genetic heterogeneity within populations. When population differentiation in *A. brachiata* reflects mostly geographical isolation and sporadic hybridisation between lineages, differentiation in *O. fragilis* could be explained by Walhund and/or selective effects. Discordance between markers observed for each brittle-star species thus provide new insights on the respective role played by population history and local processes in structuring populations. They also stress the importance of using several markers in population genetic study.

27-22 Poster

ORIGIN OF MYTILUS (MOLLUSCA, BIVALVIA) POPULATIONS FROM KERGUELEN ARCHIPELAGO INFERRED FROM MITOCHONDRIAL AND NUCLEAR DATA CONTRASTING PATTERNS

Karin Gerard [1], N. Bierne [2], P. Borsa [3], A. Chenuil [1], J.-P. Feral [1]

[1] *CNRS – Université de la Méditerranée, UMR 6540 – DIMAR, COM, Station Marine d'Endoume, Marseille, France*
[2] *CNRS – Universite Montpellier 2, UMR 5171-GPI, Station Méditerranéenne de l'Environnement Littoral, Sète, France*
[3] *UR081 – IRD, Noumea, New Caledonia*

karin.gerard@univmed.fr

The Archipelago of Kerguelen is of volcanic origin and has emerged 40 millions years ago in the Southern Ocean between the Antarctic continent and the Reunion island. It is located in the Antarctic circumpolar current, at the level of the polar front and is swept by the great west winds. At these latitudes, only the coasts of Kerguelen have fiords, which act like refuges for planktonic larvae. *Mytilus desolationis* (Lamy, 1936) that belongs to the *M. edulis* species complex has colonized all the coasts of the archipelago. Kerguelen has never been in contact with any continent. That raises the question: how and when did these *Mytilus* populations arrive there? Do these populations still recruit exogenous larvae or are they actually totally isolated ? That will determine the taxonomic status of the populations. Following nuclear DNA data, *Mytilus* population from Kerguelen shares similarities with the closely related species *M. edulis* from North Atlantic, suggesting that this population has been recently introduced from northern hemisphere by human activities. Here is presented a phylogeography of all southern *Mytilus* populations based on mtDNA sequences suggesting a totally different scenario of colonization.

27-23 Poster

PARAPATRIC VERSUS ALLOPATRIC POPULATION DIVERGENCE, AND ADAPTATION TO HYPOXIC AND NORMOXIC ENVIRONMENTS IN AN AFRICAN CICHLID

Erika Crispo [1], Lauren J. Chapman [1]

[1] *McGill University, Department of Biology, 1205 Ave. Dr. Penfield, H3A 1B1, Montreal, Canada*

erika.crispo@mail.mcgill.ca

In nature, we often observe adaptive divergence with respect to alternate selective environments within parapatric or sympatric systems. A perennial question is, how rapidly did populations adapt to alternate environments? We often question whether divergence among populations or species has occurred *in situ*, or whether multiple colonization events from allopatrically-diverged populations resulted in the observed phenotypic divergence. In this study, we test these alternate scenarios (parapatric divergence versus allopatric divergence) using parapatric populations of a haplochromine cichlid fish (*Pseudocrenilabrus multicolor victoriae*) adapted to high- (i.e. normoxic) and low-oxygen (i.e. hypoxic) conditions in Uganda. This species exhibits a variety of adaptively divergent traits in alternate environments. Areas occupied by this species have been desiccated until several thousand years ago. Adaptation to alternate environments thus either occurred *in situ* within that time frame, or it could have arisen in historically allopatric populations that have selectively colonized normoxic and hypoxic waters. We use microsatellites and mitochondrial DNA to test these alternate predictions.

27-24 Poster

THE MULTILOCUS BASED PHYLOGENETIC STUDY: INCONGRUENCE BETWEEN MITOCHONDRIAL AND NUCLEAR MARKERS IN NEOTROPICAL CICHLID FISH AND ITS IMPACT ON INTERPRETATIONS

Zuzana Musilova [1], Oldrich Rican [2], Karel Janko [3], Jindrich Novak [2]

[1] *Charles University in Prague, Department of Zoology, Vinicna 7, 12844, Prague, Czech Republic*
[2] *University of South Bohemia, Department of Zoology, Branisovska 31, 37005, Ceske Budejovice, Czech Republic*
[3] *Academy of Sciences of the Czech Republic, Institute of Animal Physiology and Genetics, Rumburska 89, 27721, Libechov, Czech Republic*

zuzmus@email.cz

The phylogenetic analysis was performed on Neotropical cichlids of the tribe Cichlasomatini. We carried out the extensive sampling covering all valid genera of this group. The sampling bias was tested using different data sets. The DNA data were analysed by commonly used distance methods, Maximum Parsimony, Maximum Likelihood and Bayesian methods and the method bias was also tested. Four molecular markers were used, both nuclear and mitochondrial, and additionally we performed multilocus AFLP analysis. We tested the incongruence between the data as well as the dependence of our results on the selected marker. We tried to differentiate the incongruence caused by selected marker from the sampling or method bias. Incongruence in the results occurred mainly in the deeper topology of phylogenetic trees causing large changes in interpretation of the evolutionary history and biogegraphic scenarios.

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27-25 Poster

NUCLEAR INTRONS GIVE EVIDENCE FOR RETICULATE SPECIATION IN THE TRITURUS CRISTATUS SUPERSPECIES

Gonçalo Espregueira Themudo [1, 2], J. W. Arntzen [3]

[1] *Naturalis - National Natural History Museum, Department of Vertebrates, P. O. Box 9517, 2300 RA, Leiden, Netherlands*
[2] *CIBIO - Centro de Investigação em Biodiversidade e Recursos Genéticos, Campus Agrário de Vairão, 4485-661, Vairão, Portugal*
[3] *Naturalis, Department of Vertebrates, P. O. Box 9517, 2300 RA, Leiden, Netherlands*

themudo@nnm.nl

The newt genus *Triturus* was recently split into several genera. The six species of marbled and crested newts that are remaining have largely parapatric distributions across Europe and the Middle East. The evolutionary history of the crested newt group (*Triturus cristatus* superspecies) is not clear. Adding to existing mitochondrial data, we developed a set of five nuclear genetic markers to elucidate the phylogeny of the group. The sample consisted of 40 individuals representing four species over their entire range. We sequenced three introns and two anonymous markers for a total of ca. 3000 bp. The reconstructed phylogeny demonstrates that the sister species *T. cristatus* and *T. dobrogicus* from northern and central Europe are relatively homogeneous, pointing to recent range expansions. *Triturus carnifex* from Italy and the Balkans shows two major geographical groups. Finally, *T. karelinii* from southeastern Europe and adjacent Asia is the most variable and is possibly a paraphyletic species. High levels of introgression and low support for interspecific relationships are evidence for reticulate speciation. We will discuss our findings in a historical biogeography context.

27-26 Poster

EVOLUTIONARY HISTORY OF TWO NEWT SUBSPECIES INFERRED FROM MULTIPLE SEQUENCE MARKERS

Krystyna Nadachowska [1], Wieslaw Babik [2]

[1] *Jagiellonian University, Institute of Environmental Sciences, ul.Gronostajowa 7, 30-387, Krakow, Poland*
[2] *Helmholtz Centre for Environmental Research - UFZ, Department of Community Ecology, Theodor-Lieser-Str. 4, D-06120, Halle/Saale, Germany*

nadachow@eko.uj.edu.pl

Information on the patterns of genetic differentiation between closely related species and divergent populations within species is essential for understanding of microevolutionary processes, as well as for conservation research. Because of incomplete lineage sorting and stochasticity of the coalescent process inferences about the historical processes and estimates of demographic parameters should be based on many unlinked loci. We analyzed the sequence variation of mitochondrial DNA (mtDNA) and nuclear markers in two subspecies of the smooth newt: *Triturus vulgaris kosswigi* and *T. v. vulgaris*. Both groups inhabit the area of south-western Turkey which is the one of the regions of glacial refugia for the *Triturus* species. However, whereas *T.v.kosswigi* distribution range is restricted to the southern coast of the Black Sea near the Bosphorus, *T.v.vulgaris* has broader distribution in Europe including both formerly glacieted and unglacieted regions. The earlier mtDNA study estimated their divergence at 2.8-3.8 Myr. To infer demographic history, patterns of gene flow and past hybridization we studied sequence variation in mtDNA five nuclear introns, one single copy non-coding nuclear marker and two nuclear genes. A suite of phylogeographic methods including phylogenetic analyses, Nested Clade Analysis and isolation with migration models of population divergence were used to asses genetic structure of populations, estimate historical population size changes and infer patterns of gene flow within and between subspecies. We found substantial genetic structure, evidence for moderate demographic growth in *T. v. vulgaris* and for demographic stability in *T. v. kosswigi*. Introgression between subspecies is geographically limited and restricted to mtDNA.

27-27 Poster

USING MITOCHONDRIAL, Y-CHROMOSOME AND AUTOSOMAL DNA MARKERS TO STUDY THE POPULATION STRUCTURE AND PHYLOGENY OF THE KHOESAN POPULATION OF SOUTHERN AFRICA

Carina M. Schlebusch [1], Himla Soodyall [1]

[1] *University of the Witwatersrand, National Health Laboratory Services, MRC, Division Human Genetics, Johannesburg, South Africa*

cschlebu@yahoo.com

The Khoesan (Khoe Khoe and San) people currently represent remnant groups of a much larger and widely distributed population of hunter gatherers and cattle herders who exclusively occupied southern Africa before the arrival of Bantu-speaking groups and sea-borne immigrants. Genetic studies on haploid markers (mitochondrial DNA and Y-chromosome) revealed that this group has retained some of the most ancient lineages found in the modern human phylogeny. Our research extends the mitochondrial and Y-chromosome DNA survey on the Khoesan by including various Khoesan sub-groups and neighboring populations for comparison. Also, a broader genetic study of variation is attempted by using autosomal SNP markers. The concordance of the haploid DNA markers versus genotypic diploid markers in shaping the gene pool of present-day Khoesan populations is also tested. Results thus far showed that autosomal SNP studies confirm the uniqueness of the genetic make-up of the Khoesan people. The Khoesan have a very distinct and deeply rooted genetic signature that distinguishes them from neighboring Bantu-speakers. Different levels of admixture from the Bantu-speaking and white populations in the different San and Khoe subgroups are also demonstrated by autosomal SNPs. In comparison to the autosomal evidence of admixture, mitochondrial markers tend to demonstrate lower levels of admixture and Y-chromosome markers higher levels. This is expected because of male biased gene flow from Bantu-speakers and white populations into Khoesan populations. Together, autosomal, mitochondrial and Y-chromosome results supports the distinctiveness of this population but also gives us a unique way of looking at historical male and female contributions versus an inclusive view.

27-28 Poster

COMBINED ANALYSIS OF FOURTEEN NUCLEAR GENES REFINES THE URSIDAE PHYLOGENY

Marie Pagès [1, 2], Sébastien Calvignac [1], Catherine Klein [1], Mathilde Paris [3], Sandrine Hughes [1], Catherine Hänni [1]

[1] *University of Lyon, Paleogenetics and Molecular Evolution Team, Institute of Functional Genomics, F-69003, France; INRA, CNRS, University of Lyon 1, Ecole Normale Supérieure, F-69364, France*

[2] *University Montpellier II, Paleontology, Phylogeny and Paleobiology Team, Institute of the Sciences of the Evolution, UMR CNRS 5554, Place Eugène Bataillon, 34095 Montpellier Cedex 05, France*

[3] *University of Lyon, Molecular Zoology Team, Institute of Functional Genomics, F-69003, France; INRA, CNRS, University of Lyon 1, Ecole Normale Supérieure, F-69364, France*

Marie.Pages@ens-lyon.fr

To definitively solve the last the ambiguities concerning the evolutionary history of Ursidae, we sequenced ten nuclear genes for all the eight extant bear species. By combining these new sequences with those of four other recently published nuclear markers, we provide new insights into the phylogenetic relationships of the Ursidae family members. The hypothesis that the giant panda was the first species to diverge among ursids is definitively confirmed and the branching order within the *Ursus* genus is clarified for the first time. Moreover, these analyses indicate that the American and the Asiatic black bears do not cluster as sister taxa, as had been previously hypothesised. Sun and sloth bears undoubtedly appear as the most basal ursine species but uncertainties about their exact relationships remain.

27-29 Poster

A GENOMIC APPROACH TO THE COMPLEX EVOLUTIONARY RELATIONSHIPS IN THE GENUS MICROTUS

Martin C. Fischer [1], Sabine Fink [1], Laurent Excoffier [1], Gerald Heckel [1]

[1] *University of Bern, Zoological Institute, CMPG, Baltzerstrasse 6, CH-3012, Bern, Switzerland*

martin.fischer@zoo.unibe.ch

Molecular phylogenies based on mitochondrial sequence (mtDNA) data are often used to try to solve problems concerning systematic relationships and evolutionary histories. It is important to consider that a single locus may not necessarily represent the evolutionary history correctly. We investigate here the rapid and ongoing radiation in the vole genus *Microtus* which produced about 70 species within the last 1.2 to 2 million years. Due to an initial burst of speciation, it has proven difficulty to resolve the basal evolutionary relationships – mainly the colonization history of America, Asia and Europe – within this genus. We analyzed a battery of AFLP to reconstruct phylogenetic relationships in comparison with a nuclear sequence marker (coding sequence in exon 1 of the nuclear arginine-vasopressin 1a receptor gene and corresponding non-coding 5' flanking region) as well as the mitochondrial cytochrome *b* (cytb) gene. More than 20 species across the entire distribution range of *Microtus* were analyzed and *Arvicola terrestris* was used as an outgroup. The resulting phylogenetic patterns are discussed in regard to the evolutionary history of the genus and the advantage and disadvantage of single locus and genomic approaches.

27-30 Poster

THE ORIGIN OF THE ORKNEY VOLE

Natália Martínková [1, 2], Gerald Heckel [3], Keith Dobney [4], Jeremy B. Searle [1]

[1] *University of York, Department of Biology, PO Box 373, YO10 5YW, York, United Kingdom*
[2] *Institute of Vertebrate Biology AS CR, v.v.i., Department of Population Biology, Studenec 122, 675 02, Kon?šín, Czech Republic*
[3] *University of Bern, Computational and Molecular Population Genetics (CMPG), Zoological Institute, Baltzerstrasse 6, CH-3012, Bern, Switzerland*
[4] *University of Durham, Department of Archaeology, South Road, DH1 3LE, Durham, United Kingdom*

martinkova@brno.cas.cz

The common vole (Microtus arvalis) is a widespread and abundant species in Europe. It is absent from Great Britain and Ireland, but occurs on seven islands of the Orkney archipelago where it is distinguished as a separate subspecies. Orkney voles (M. a. orcadensis) were probably transported by humans from continental Europe to Orkney in the Neolithic. We sequenced the mitochondrial gene for cytochrome b and SMCY7 intron located on Y chromosome to identify better the source area of Orkney voles. They originated from northern France/Belgium, not from Spain or the Pyrenees region as has been proposed previously. Voles from other lineages occur in the Netherlands and Denmark. No recent introduction between Orkney and continental Europe has been detected. We will describe how phylogenetics and molecular diversity indices may be used to study the pattern of colonisation within the Orkney archipelago.

27-31 Poster

DISCORDANT EVOLUTION OF KARYOTYPE AND GENETIC DIVERGENCE IN MICROTUS SUBTERRANEUS

Natália Martínková [1, 2], Carl-Johan Andersson [3], Gerald Heckel [4], Maarit Jaarola [5]

[1] *Institute of Vertebrate Biology AS CR, v.v.i., Department of Population Biology, Studenec 122, 675 02, Kon?šín, Czech Republic*
[2] *University of York, Department of Biology, PO Box 373, YO10 5YW, York, United Kingdom*
[3] *Lund University, Department of Cell and Organism Biology, Sölvegatan 29, SE-223 62, Lund, Sweden*
[4] *University of Bern, Computational and Molecular Population Genetics (CMPG), Zoological Institute, Baltzerstrasse 6, CH-3012, Bern, Switzerland*
[5] *Polish Academy of Sciences, Mammal Research Institute, ul. Waszkiewicza 1c, 17-230, Bia?owie?a, Poland*

martinkova@brno.cas.cz

European pine vole (Microtus subterraneus) exhibits the highest within-species genetic variability among the representatives of subgenus Terricola and two karyomorphs are known (2N = 52 and 54). Populations of voles with 52 chromosomes occur at the centre of the distribution, whereas those with 54 chromosomes are found at range peripheries. We sequenced genetic markers with maternal (mitochondrial DNA) and paternal inheritance (Y chromosome) as well as markers on the X chromosome that are inherited from both parents. We found deeply divergent evolutionary lineages congruent among molecular markers, which do not correspond to the distribution of the two karyomorphs. Divergence between Europe and Asia Minor is smaller than divergence within the Turkish part of the M. subterraneus distribution. The lineage that colonised the largest area is spread across Central and Western Europe. Our data indicate that M. subterraneus survived the last glaciation in multiple refugia in Turkey and Europe. These results are discussed in regard to the role of glacial cycles for the rapid speciation processes in the genus Microtus.

27-32 Poster

ANALYSES OF MTDNA, Y AND X CHROMOSOME SEQUENCES REVEAL CONGRUENT PHYLOGEOGRAPHIC STRUCTURE IN ARCTIC LEMMINGS (LEMMUS)

Vadim B. Fedorov [1], Anna V. Goropashnaya [1]

[1] *University of Alaska Fairbanks, Institute of Arctic Biology, 311 Irving 1, 99709, Fairbanks, Alaska*

fnvf@uaf.edu

Arctic lemmings demonstrated strong mtDNA phylogeographic structure across Holarctic with the three significant longitudinal divisions. The depth of phylogeographic splits (mtDNA cytochrome b net divergence 8.7%; 6.2% and 4.5%) suggests continuous vicariant separation over several glacial-interglacial periods. In order to confirm independent evolutionary history of the phylogeographic groups detected by mtDNA variation, we studied sequence variation in introns of Y and X chromosomes. Reciprocal monophyly of all groups revealed by variation in maternal mtDNA marker was supported by genealogy based on variation in paternal Y chromosome. Genealogy based on variation in biparental X chromosome was congruent to the mtDNA and Y chromosome phylogenies, with exception for non reciprocal monophyly of the two Eurasian phylogeographic groups. This probably indicates incomplete lineage sorting due to three times lager effective size for X chromosome. Similar to other mammalian species, nucleotide diversity estimates were highest for mtDNA (7.3%), X chromosome (1.1%) and lowest for Y chromosome (0.7%). To investigate extent of introgression, we screened variation in all three markers across an area of secondary contact between the Beringian and Eastern phylogroups in east Alaska – Yukon. Analysis of 65 lemmings, including 44 males, detected 11 hybrids (17%) and possibly indicated existence of some reproductive barriers. These results show that analysis with the three different types of genetic markers facilitates inference on evolutionary history. However, resolving power of X and Y chromosome markers is limited by low levels of genetic variation.

27-33 Poster

BROWN RAT (RATTUS NORVEGICUS) POPULATION STRUCTURE IN ENGLAND

Haniza H. Mohd. Zain [1], Sally Adams [1], Eamonn B. Mallon [1]

[1] *University of Leicester, Biology, University Road, LE1 7RH, Leicester, United Kingdom*

hhm1@le.ac.uk

The brown rat, *Rattus norvegicus* is one of the most important vertebrate pest species in England. Extensive use of rodenticides as a method of protection against rats infestation in farms has led to the evolution of resistance. The rate at which resistance is acquired is a function of the resistance allele's frequency, its dominance, the relative fitness of being resistant and often overlooked the pest organism's population structure. My research is to understand the genetic structure of rat populations in the England agricultural landscape. Mitochondrial DNA and microsatellite DNA were used to identify the gene flow between counties and between farms populations. We discuss our results in the light of the gene flow and the population divergence.

27-34 Poster

THE BOOK OF INVASIONS: PHYLOGEOGRAPHY OF PYGMY SHREWS (SOREX MINUTUS) IN IRELAND AND EUROPE.

Allan D. McDevitt [1], Victor Rambau [2], Thomas J. Hayden [1], Glenn Yannic [3], Jeremy B. Searle [4]

[1] *University College Dublin, School of Biology & Environmental Science, Belfield, Dublin 4, Ireland*
[2] *Stellenbosch University, Department of Botany and Zoology, South Africa*
[3] *University of Lausanne, Department of Ecology and Evolution, Lausanne, Switzerland*
[4] *University of York, Department of Biology, York, United Kingdom*

allan.mcdevitt@ucd.ie

Whether or not the pygmy shrew is a native species to Ireland has been the subject of much debate. If not native, from where and by what means did it colonise Ireland? In order to answer these questions, an 800bp fragment of the control region of the maternally inherited mitochondrial genome and four introns of the paternally inherited Y chromosome (3kb) have been sequenced from pygmy shrews throughout Ireland, Britain and Western Europe. This study is also incorporating the use of five microsatellite loci (biparental markers) to compare genetic diversity and possible gene flow between Ireland and Britain.

According to the mtDNA sequence data, the majority of Britain and central/northern Europe appears to have been colonised from a glacial refuge in central Europe while Ireland was colonised from northern Iberia/southern or central France. However, according to the Y chromosome sequence data, both British and Irish pygmy shrew populations have an Iberian origin. Microsatellite data also suggests that Ireland is a subset of the British population as all alleles found in Ireland are also found in Britain, with no alleles unique to Ireland.

Although the Irish population belongs to the Iberian lineage, our data shows that Ireland was most likely colonised from its nearest landmass, Britain. This study highlights the importance of using multiple genetic markers when inferring the phylogeographic structure and colonisation history of species.

27-35 Poster

THE COLONISATION OF IRELAND – MYTHS, MYSTERY AND MOLLUSCS

Adele J. Grindon [1]

[1] *University of Nottingham, Institute of Genetics, Q.M.C., NG7 2UH, Nottingham, England*

plxag2@nottingham.ac.uk

It has long been recognised that the flora and fauna of Ireland has a characteristic "Lusitanian" element, as several species are only found in Ireland and Iberia. Although the land snail *Cepaea nemoralis* is widespread across Europe, it has been suspected that some populations of the west coast of Ireland may have a Spanish, specifically Pyrenean, origin because of their characteristic morphology. In order to clarify the origin of the Irish *C. nemoralis* I have obtained molecular sequence data for this species. Over 500 individuals from 41 separate locations across Western Europe were collected and a fragment of the mitochondrial gene cytochrome oxidase subunit I (COI) sequenced. Phylogenetic analysis of these sequences reveals that populations from western Ireland probably originate from a source in the Spanish Pyrenees, supporting similar findings with the Irish pygmy shrew. In contrast, individuals in the south-west of Ireland have a common origin with populations from western Britain and France, however individuals from the same Irish population also share a similar haplotype with populations in Northern Spain. Given that fossil data indicates that *C. nemoralis* has been in Ireland for about 8000 years, the significance of these findings in relation to the post-glacial colonisation of Ireland will be discussed.

27-36 Poster

MITOCHONDRIAL AND NUCLEAR GENEALOGIES REVEAL A HISTORY OF RANGE FRAGMENTATION FOLLOWED BY EXPANSION AND SECONDARY CONTACT IN THE BLACK SPINY TAILED IGUANA (CTENOSAURA PECTINATA).

Eugenia Zarza-Franco [1], Victor H. Reynoso [2], Brent C. Emerson [1]

[1] *University of East Anglia, School of Biological Sciences, UEA, NR4 7TJ, Norwich, United Kingdom*
[2] *Universidad Nacional Autonoma de Mexico, Coleccion Nacional de Anfibios y Reptiles, Instituto de Biologia, Ciudad Universitaria, 04510, DF, Mexico*

g.zarza-franco@uea.ac.uk

The threatened iguana species *Ctenosaura pectinata* is endemic to Mexico, inhabiting a wide variety of environments throughout its broad distribution along the Pacific coast and Río Balsas Basin. We have sampled *C. pectinata*, and related species, extensively from across their geographic distribution for phylogeographic analysis. Phylogenetic trees and networks constructed from mitochondrial DNA sequence data indicate strong genetic divergence between five geographic lineages within *C. pectinata*. Some of these lineages form zones of secondary contact, and one forms a contact zone with *C. hemilopha,* with both genetic and morphological evidence of hybridisation. Relatively small genetic distances are found between populations of *C. acanthura* and *C. pectinata*, bringing into question the taxonomic status and evolutionary origin of *C. acanthura*. Conclusions from mtDNA are supported by genealogical analyses of nuclear sequence data from the enolase gene. Together both mtDNA and nuclear sequence data reveal the oldest populations of *C. pectinata* to be those of the northern and southern coastal regions. Inland and mid-latitudinal coastal populations are younger in age as a consequence of a history of local extinction within these regions followed by recolonisation. Estimation of divergence times suggest that divergences within *C. pectinata* are reflective of climatic and geological influences prior to the Pleistocene.

27-37 Poster

GENE FLOW ACROSS A NARROW AND HIGHLY DIVERGENT MTDNA CONTACT ZONE IN THE SIDE-BLOTCHED LIZARD (UTA STANSBURIANA) OF BAJA CALIFORNIA, MEXICO

Johan Lindell [1, 2], Fausto R. Méndez-de la Cruz [3], Robert W. Murphy [1, 2]

[1] *University of Toronto, Department of Ecology & Evolutionary Biology, 25 Willcocks Street, M5S 3B2, Toronto, Ontario, Canada*
[2] *Royal Ontario Museum, Department of Natural History, 100 Queen's Park, M5S 2C6, Toronto, Ontario, Canada*
[3] *Universidad Nacional Autónoma de México, Instituto de Biología, A.P. 70-153, C.P. 04510, México, D.F., Mexico*

johan.lindell@utoronto.ca

The peninsula of Baja California of northwestern Mexico has a complex geological history that has greatly affected its biota. Noticeably, seaways have cut across the peninsula since late Miocene, temporarily isolating populations. These events have left a genetic trace as evident from the congruent mtDNA genealogies of numerous species. In the side-blotched lizard (Uta stansburiana), two highly divergent (10% sequence divergence in cytochrome b) mtDNA lineages meet in an old secondary contact zone midway on the peninsula. Geographically detailed analyses show that mtDNA introgression is extremely limited across the contact zone, a pattern potentially associated with overall population divergence, development of reproductive isolation, and speciation. However, nuclear gene flow appears to be widespread along the peninsula in numerous species affected by the same vicariant history. We discuss genetic divergence across the mid-peninsular contact zone of U. stansburiana based on mtDNA sequence data and variation in microsatellite DNA loci. In addition, we describe patterns of cytonuclear discordance along the entire peninsula, emphasizing the differences between maternal and biparental histories and their relevance to historical biogeography and estimates of population differentiation.

27-38 Poster

WHY SHOULD WE EXPECT A LOWER GENETIC STRUCTURE FOR ORGANELLE DNA COMPARED TO NUCLEAR DNA IN HYBRIDIZING SPECIES PAIRS? EXAMPLE OF TWO ZONES OF SECONDARY CONTACT BETWEEN LARGE GULL SPECIES.

Laurene Gay [1], Pierre-Andre Crochet [2]

[1] *University of Exeter Cornwall, Centre for Ecology and Conservation, TR10 9EZ, Penryn, UK*
[2] *Centre d'Ecologie Fonctionnelle et Evolutive, 1919 route de Mende, 34293, Montpellier, France*

l.gay@exeter.ac.uk

In zones of secondary contact, any gene involved in the reproductive barriers will be less prone to introgression than neutral markers. Recent studies have shown that these genes are frequently located on sex chromosomes. Furthermore, sex-biased dispersal, behaviour generating pre-mating barriers or sex-specific post-mating barriers also result in sex-biased introgression. We thus expect to observe a lower rate of introgression in sex-linked DNA such as organelle DNA compared to nuclear DNA. This could create conflicts between the evolutionary histories inferred from cytoplasmic and nuclear markers.

We first reviewed the published instances of sex-biased introgression in hybrid zones. Then, we compared introgression patterns for microsatellite loci, a fragment of mitochondrial DNA and a set of phenotypic traits known to be involved in reproductive isolation, in two zones of recent secondary contact between large gull species.

In the American hybrid zone, the cline on mitochondrial haplotypes did not differ significantly from the clines in nuclear allele frequencies in centre or slope. The introgression rate for phenotypic traits was lower compared to both nuclear and mitochondrial markers. However, in the European hybrid zone, cyto-nuclear linkage analyses detected asymmetric introgression of mitochondrial DNA and suggested that interspecific crosses may be more successful in one direction.

We finally discuss the implication of sex-biased introgression for the nuclear and mitochondrial genetic structure. This study emphasizes that multi-locus approaches are useful to identify barriers to gene flow in hybrid zones.

27-40 Poster

RECONCILING ANCIENT REFUGIA WITH RECENT GENE FLOW IN GIANT PETRELS

Mareile N. M. S. Techow [1, 2], Peter G. Ryan [1], Colleen O'Ryan [2]

[1] University of Cape Town, DST/NRF Centre of Excellence at the Percy FitzPatrick Institute, Private Bag, Rondebosch, 7700, Cape Town, South Africa
[2] University of Cape Town, Molecular and Cell Biology, Private Bag, Rondebosch, 7700, Cape Town, South Africa

techow@science.uct.ac.za

There are two species of giant petrels (*Macronectes*), both of which are endangered as a result of the long-line fishing industry. Species status of the two forms has been debated, and it has been concluded that their divergence is recent. Mitochondrial cytochrome b sequences and microsatellite data were used to assess their evolutionary history and to investigate whether contemporary gene flow occurs. Cytochrome b sequences confirmed that species divergence is indeed recent, with a very low sequence divergence (0.78%). Northern Giant Petrels (NGP) form a monophyletic group, but the Southern Giant Petrel (SGP) is paraphyletic, with a sister clade to both NGP and most SGP haplotypes. However, preliminary microsatellite analysis shows complete nuclear segregation between the two species, indicating gene flow is largely confined to within currently-defined species. Recently evolved species present a problem for interpreting neutral variation because lineage sorting is driven by genetic drift. Therefore the concordance between morphological and gene phylogenies is dependant on time and demographic events, and may result in the lack of diagnostic lineage sorting even in the presence of barriers to gene flow. In this event, separate species may be identified by differences in allele frequencies and the use of both mitochondrial and nuclear data may yield valuable insights otherwise lost to gene trees alone. Mismatch distributions of the giant petrels identified two expansions in the SGP, one old (3.6 – 12.3. myr) and the other more recent (0.6 – 2.0 myr), occurring at the same time as the expansion in the NGP. This suggests that the SGP experienced fragmentation perhaps through a period of glacial maxima leading to later expansion and speciation as well as secondary contact of lineages within the SGP.

27-41 Poster

POPULATION HISTORY OF AN OCEANIC ENDEMIC BIRD; RECENT DISPERSAL, CONTEMPORARY GENE FLOW AND THE ROLE OF DRIFT AND SELECTION IN MORPHOLOGICAL DIVERGENCE

Juan C. Illera [1], Brent C. Emerson [1], David S. Richardson [1]

[1] University of East Anglia, Centre for Ecology, Evolution and Conservation, School of Biological Sciences, NR4 7TJ, Norwich, United Kingdom

j.illera@uea.ac.uk

We investigate diversification and incipient speciation using Berthelot’s pipit (*Anthus berthelotii*), an endemic bird species whose metapopulation spans three Atlantic archipelagos. Mitochondrial DNA (mtDNA) and microsatellite markers were used to deduce the pathway by which this species colonised the islands and to determine gene flow and genetic differentiation among the 12 island populations. Morphological differentiation across the islands was also examined. An absence of mtDNA variation (only one haplotype was found) suggests that the Berthelot’s pipit has only recently dispersed throughout the Macaronesian islands. However, microsatellite allele frequency data indicate population differentiation ($F\text{st} = 0.069$) between archipelagos -the three archipelagos were identified as genetically distinct units. Both phylogenetic analysis and variability in allelic richness between populations suggests that the pipit originally colonised the Canary Islands and then spread northwards to the Madeira archipelago and Selvagen Islands. Morphological differences were also consistent between archipelagos although the differences recorded could be due to island specific selective pressures. Patterns of concordance between morphological and genetic differentiation provided ambiguous results suggesting that drift alone could not be sufficient to explain phenotypic differentiation. The metapopulation of Berthelot’s pipit may therefore provide an example of a species undergoing incipient speciation and an adaptive radiation.

Ecological and evolutionary immunology

28

Wednesday August 22 *Location*: University building X

Symposium 28: Ecological and evolutionary immunology

ORGANIZERS: Yannick Moret, Université de Bourgogne, France
Michael Siva-Jothy, University of Sheffield, UK
Joachim Kurtz, ETH-Zentrum, Switzerland
Hinrich Schulenburg, University of Tübingen, Germany

9.45-10.15	**Louis Du Pasquier** (invited) Germline and somatic diversification of immune repertoires in Metazoa
10.15-10.45	**Tom Little** (invited) The cost and benefit of the immune response in Daphnia
10.45-11.05	**Daniela Brites** A diversified Dscam homologue in the Crustacean Daphnia
11.05-11.35	*Coffee*
11.35-11.55	**Livia Roth** Can beetles be vaccinated?
11.55-12.15	**Ruth Hamilton** Parasite diversity selects for combined inducible and constitutive immune responses in a model of innate immunity
12.15-12.35	**Lena Wilfert** The genetic architecture of immune defence and reproduction in male Bombus terrestris bumblebees
12.35-14.00	*Lunch, council*
14.00-14.30	**Paul Schmid-Hempel** (invited) Immune defence, pathogenesis and some unsettled questions
14.30-14.50	**Jenny Bangham** High levels of genetic variation in the susceptibility of Drosophila melanogaster to viral infection are caused by major-effect polymorphisms
14.50-15.10	**Rebecca Schulte** Experimental coevolution of Caenorhabditis elegans and its microparasite Bacillus thuringiensis
15.10-15.30	**Lars Råberg** Resistance and tolerance to parasites in animals
15.30-16.00	*Coffee*
16.00-16.20	**Jouni Taskinen** Do measures of immunocompetence measure immunocompetence?
16.20-16.40	**Natalia Pitala** Nestling immune response to phytohaemagglutinin is not heritable in collared flycatchers
16.40-17.00	**Sylvia Cremer** Social prophylaxis: collective immunity in ant societies
17.00-17.20	**Brian Preston** Sleep and the mammalian immune system

28-01 Talk

GERMLINE AND SOMATIC DIVERSIFICATION OF IMMUNE REPERTOIRES IN METAZOA

Louis Du Pasquier [1]

[1] *University of Basel, Institute of Zoology and Evolutionary Biology, Switzerland*

dupasquier@dial.eunet.ch

A basic diversity of potential immune-receptor genes existed in primitive Metazoa. Polymorphism, duplication and somatic mechanisms of diversification affected independently and still affect different gene families in many phyla, creating a greater variety of immune systems exhibiting sometimes little homology but much analogy to one another. Diversity and multiplicity of receptors was generated by duplication and creation of multigene families. Independently in several phyla further diversity is created somatically in some selected categories of receptors by alternate splicing, somatic mutation, gene conversion and gene rearrangement. In several instances combinatorial usage of polypeptide chains or genes segments increases further the repertoire of the recognition structures. Metazoa had to adapt to the conditions generated by this diversity, control the expression of multigene family members on the cell surface, and generate processes of selection to control the risk of autoimmunity.

28-02 Talk

A DIVERSIFIED DSCAM HOMOLOGUE IN THE CRUSTACEAN DAPHNIA

McTaggart Seanna [1], Daniela Brites [2], Little Tom [1], Dieter Ebert [2], Louis Du Pasquier [2]

[1] *University of Edinburgh, Evolutionary Biology, Room 413, Ashworth Laboratory, Edinburgh, Uk*
[2] *University of Basel, Evolutionary Biology, Vesalgasse 1, 42051, Basel, Switzerland*

d.brites@unibas.ch

The Down syndrome cell adhesion molecule (Dscam) gene is present from plathyhelmintes to vertebrates, playing a role in controlling neural wiring. The Dscam gene of insects is one of the most dramatic examples known of protein diversity generated by alternative splicing of multiple exon copies from a single gene. The exons coding for half of 2nd , 3rd and the whole 7th Immunoglobulin domains and 2 exons coding for the transmembrane domain of the molecule undergo mutually exclusive alternative splicing, generating a high diversity of transcript forms (> 38000 in *D. melanogaster*). The alternative splicing is also implicated in the immunity of insects which, given the tremendous variation of the molecule, suggests that it could act in an analogous way to vertebrate antibodies. The completion of *Daphnia pulex* genome sequencing, allowed to determine the genetic structure of its Dscam gene and to compare it to that of other species. It is organized like in *Drosophila,* i.e. with clusters of exons coding for the Ig domains 2,3 and 7. We could isolate by reverse transcriptase PCR Dscam transcripts from brain and hemocytes, showing that *Daphnia* expresses Dscam variability in both tissues. This suggests that the role of diversity in the nervous and immune system is conserved. So far, highly diversified DSCAM exists only in Artropods. Why is Dscam diversified only in this group? What was the original driving factor that selected the alternative exon usage strategy? Comparative studies, using functional as well as a phylogenetic approach, could help to resolve at least some of these questions.

28-03 Talk

CAN BEETLES BE VACCINATED?

Livia Roth [1], Benjamin M. Sadd [1], Gerrit Joop [1], Joachim Kurtz [2]

[1] *ETH Zürich, Experimental Ecology, Universitätsstrasse 16, 8092, Zürich, Switzerland*
[2] *University of Münster, Institute for Evolution and Biodiversity, Universitätsstrasse 16, 8092, Münster, Germany*

olivia.roth@env.ethz.ch

Recent data indicates that, contrary to prior belief, invertebrates are capable of specific immune priming. However, as yet we lack an in-depth analysis of the degree of specificity and the duration of these immune reactions. This question is especially relevant in holometabolous insects, where the physiological changes and reorganization of the whole body during the pupal stage may prevent the persistence of priming effects from the larval into the adult stage. On the other hand, the specificity of immunological memory may increase over time, as is observed during affinity maturation in the vertebrate immune system. Furthermore, it is still unclear, whether the humoral or the cellular immune response mediates specificity. In our experiment, young larvae of the red flour beetle Tribolium castaneum are primed with various species of killed bacteria. Individuals will then be challenged with live bacteria, after different time intervals. Several measures of resistance and immunity will serve to compare beetles that were primed and challenged with the same rather than different species of bacteria. This will allow testing for the specificity and the duration of the humoral and the cellular immune response.

28-04 Talk

PARASITE DIVERSITY SELECTS FOR COMBINED INDUCIBLE AND CONSTITUTIVE IMMUNE RESPONSES IN A MODEL OF INNATE IMMUNITY

Ruth B. Hamilton [1], Michael T. Siva-Jothy [1], Mike Boots [1]

[1] *University of Sheffield, Department of Animal and Plant Sciences, Western Bank, S10 2TN, Sheffield, United Kingdom*

r.hamilton@sheffield.ac.uk

Parasites represent a major threat to all organisms which has lead to the evolution of an array of complex and effective defence mechanisms. Common to both vertebrates and invertebrates are innate immune mechanisms that can be either constitutively expressed or induced on exposure to infection. In nature we find that a combination of both induced and constitutive responses are employed by vertebrates, invertebrates, and, to an extent, plants when they are exposed to a parasite. Here we use a simple within-host model motivated by the insect immune system, consisting of both a constitutive and induced response, to address the question of why both types of responses are maintained so ubiquitously. Generally, induced responses are thought to be advantageous because they are only used when required but are too costly to maintain constantly, while constitutive responses are advantageous because they are always ready to act. However, using a simple cost function but with no a priori assumptions about relative costs, we show that variability in parasite growth rates selects for a strategy that combines both constitutive and induced defences. Differential costs are therefore not necessary to explain the adoption of both forms of defence. Clearly, hosts are likely to be challenged by variable parasites in nature and this is sufficient to explain why it is optimal to deploy both arms of the innate immune system.

28-05 Talk

THE GENETIC ARCHITECTURE OF IMMUNE DEFENSE AND REPRODUCTION IN MALE BOMBUS TERRESTRIS BUMBLEBEES

Lena Wilfert [1], Juergen Gadau [2], Paul Schmid-Hempel [1]

[1] *ETH Zürich, IBZ, Universitätsstrasse 16, 8092, Zürich, Switzerland*
[2] *Arizona State University, School of Life Sciences, AZ 85287-4501, Tempe, USA*

lena.wilfert@env.ethz.ch

Understanding the architecture of genetic variation, i.e. the number, effect, location and interaction, of genes responsible for phenotypic variability in nature is important for the understanding of micro-evolutionary processes. In this study, we have used a QTL approach to uncover the genetic architecture of fitness-relevant traits associated with reproduction and immune defense in male B. terrestris bumblebees. Three male reproductive investment traits, the number and length of the produced sperm and the size of the accessory glands, were studied. Two branches of the insect innate immune system, the activation of the Phenoloxidase-cascade and the hemolymph's antibacterial activity, were investigated. We found that variation in most of the studied traits is based on a network of minor QTLs and epistatic interactions. Unexpectedly, there was no evidence for phenotypic or genetic trade-offs between the presumably costly investment in immune defense and reproductive effort in this population for the measured traits. In fact, we found a positive correlation, both, in phenotype and genetic architecture for the number of produced sperm and antibacterial activity against an insect pathogen. By comparing genetic information from bumblebees with the honeybee genome, we are exploring potential candidate genes underlying QTLs for the activation of the Phenoloxidase-cascade.

28-06 Talk

HIGH LEVELS OF GENETIC VARIATION IN THE SUSCEPTIBILITY OF DROSOPHILA MELANOGASTER TO VIRAL INFECTION ARE CAUSED BY MAJOR-EFFECT POLYMORPHISMS

Jenny Bangham [1], Francis Jiggins [1]

[1] *University of Edinburgh, Institute of Evolutionary Biology, UK*

jenny.bangham@ed.ac.uk

A great deal of genetic variation affects susceptibility to pathogens in a wide range of organisms. We have made some detailed studies of genetic variation in antiviral resistance using *Drosophila melanogaster* and its natural pathogen, the sigma virus. We have found that both susceptibility to infection by the virus and transmission of the virus are affected by considerable genetic variation, and that much of this variation is caused by major effect polymorphisms. One particularly important gene is *ref(2)P* — a polymorphic gene already known to affect sigma transmission and replication. We have confirmed previous findings that a single complex mutation in the gene *ref(2)P* confers resistance against sigma, and show that this mutation has increased in frequency under positive selection. We have also found a second locus with a major effect on these traits, by carrying out three quantitative trait loci (QTL) analyses to map the loci responsible for genetic variation in sigma transmission.

28-07 Talk

THE COST AND BENEFIT OF THE IMMUNE RESPONSE IN DAPHNIA

Tom J. Little [1]

[1] *University of Edinburgh, Institute of Evolutionary Biology, EH9 3JT, Edinburgh, United Kingdom*

tom.little@ed.ac.uk

The deployment of the immune system has the obvious potential to ameliorate infection outcomes, but immune responses can also harm hosts by either damaging host tissues or monopolising resources, leading to enhanced mortality. To gain insight into such a 'cost of immunity' when the crustacean Daphnia magna is challenged with the bacterium Pasteuria ramosa, we measured survivorship among hosts that were exposed to various strains and doses of P. ramosa, but resisted infection. Survivorship was reduced if hosts were exposed to relatively non-pathogenic strains; it was reduced further if there were two rounds of exposure to these non-pathogenic strains; it was reduced further still when hosts resisted relatively aggressive parasite strains. In a separate experiment, resisting infection to a large dose of an aggressive P. ramosa strain resulted in greater mortality than when a medium or low dose was resisted. Assuming that resistance is accomplished with an immune response, and that more aggressive parasites and larger doses of parasites are more immunostimulatory, these data are compatible with a cost of immunity. Indeed, in terms of survival, resisting parasites appeared more harmful than infection. However, in a related experiment, we showed that resisting parasites could be beneficial upon a secondary challenge, i.e. the primary exposure made hosts more resistant, although this was highly dependent on the particular parasite strain used. In all of this, we have so far assumed that an actual immune response underlies these effects, but this may not be so. Hopefully this talk will end with data from preliminary measurements of the Daphnia immune response.

28-08 Talk

EXPERIMENTAL COEVOLUTION OF CAENORHABDITIS ELEGANS AND ITS MICROPARASITE BACILLUS THURINGIENSIS

Rebecca D. Schulte [1], Carsten Makus [2], Barbara Hasert [2], Nico K. Michiels [1], Hinrich Schulenburg [1]

[1] *University Tuebingen, Animal Evolutionary Ecology, Auf der Morgenstelle 28, 72076, Tuebingen, Germany*
[2] *University Muenster, Institute for Evolution and Biodiversity, Huefferstrasse 1, 48149, Muenster, Germany*

rebecca.schulte@uni-tuebingen.de

The continuous interaction between a host and a parasite results in extremely strong selection pressure on both partners. As soon as the host evolves an efficient defence, the parasite will alter infection and/or virulence mechanisms, which is again followed by the evolution of new host defences, potentially leading to a coevolutionary arms race (Red Queen hypothesis). Thus, host-parasite coevolution should be characterised by highly dynamic changes over time, which are likely to affect a diversity of life-history traits (in addition to defence and virulence). However, due to the scarcity of suitable experimental systems, the underlying mechanisms and the resulting consequences are only poorly understood. For this reason, we performed a laboratory-based selection experiment, in which the nematode *Caenorhabditis elegans* was forced to interact with its microparasite *Bacillus thuringiensis* at different levels. After 48 generations hosts that coevolved with parasites were found to be more resistant compared to hosts evolving in the presence of a non-pathogenic control bacterium. Similarly, coevolved parasites increased in virulence. At the same time, coevolved hosts and parasites both showed reduced reproductive rates, strongly suggesting a cost for resistance and virulence. Genetic data further supported enhanced evolutionary rates in the coevolution treatment. Taken together, the results provide novel insights into the diverse consequences of coevolutionary interactions between host and parasite.

28-09 Talk

RESISTANCE AND TOLERANCE TO PARASITES IN ANIMALS

Lars Råberg [1], Derek Sim [2], Andrew Read [2]

[1] Lund University, Animal Ecology, Ecology Building, 223 62, Lund, Sweden
[2] University of Edinburgh, Institute of Immunology and Infection Research, West Mains Road, EH9 3JT, Edinburgh, UK

lars.raberg@zooekol.lu.se

Defence against pathogenic micro-organisms and other parasites can be divided into two conceptually different types: resistance (the ability to limit parasite burden) and tolerance (the ability to limit the disease severity of a given parasite burden). It is important to distinguish between these two types because, by definition, resistance has a negative effect on parasites while tolerance does not; as a result, their relative importance will have significant consequences for the ecology and evolution of host-parasite interactions. While studies of plant-parasite systems have shown genetic variation for both these types of defence, studies of genetic variation for defence in animal host-parasite systems have so far focused on resistance, or not distinguished between the two. Here, we use the statistical framework for analysis of host defence developed in the plant literature to formally disentangle genetic variation for resistance and tolerance in an animal host-parasite system— the rodent malaria parasite *Plasmodium chabaudi* in inbred strains of laboratory mice. We found that mouse genotypes vary not only in resistance but also in tolerance, as measured by the degree of red blood cell and weight loss with increasing infection intensity. Moreover, the two components of defence were negatively correlated across mouse genotypes.

28-10 Talk

DO MEASURES OF IMMUNOCOMPETENCE MEASURE IMMUNOCOMPETENCE?

Jouni Taskinen [1], Anssi Vainikka [2], E. Ilmari Jokinen [3], Katja Löytynoja [3], Raine Kortet [4]

[1] University of Joensuu, Ecological Research Institute, P.O. Box 111, FI-80101, Joensuu, Finland
[2] Swedish Board of Fisheries, Institute of Coastal Research, SE-74071, Öregrund, Sweden
[3] University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FI-40014, Jyväskylä, Finland
[4] University of Oulu, Department of Biology, P.O. Box 3000, FI-90014, Oulu, Finland

jouni.taskinen@joensuu.fi

Various measures of immune function are being used in immunological ecology. How well do those measures actually reveal the competence of immune defense, i.e. individual's ability to eliminate or control parasites? We combined nine measures of immune function of the wild cyprinid fish, roach (*Rutilus rutilus* L.)—relative counts of (1) lymphocytes, (2) thrombocytes, (3) granulocytes and (4) macrophages, (5) total IgM concentration, (6) relative mass of the spleen, (7) total count of leukocytes in blood, (8) chemiluminescence and (9) migration differential of head kidney phagocytes)—into three principal components, and studied their correlations with the load of four most prevalent parasite species (*Rhipidocotyle campanula*, *R. fennica*, *Raphidascaris acus* and *Diplostomum spathaceum*) and a viral disease, papillomatosis, and with the proportion of dead *R. campanula*. Principal components describing relative counts (granulocytes and macrophages) and functional aspects (respiratory burst, migration) of phagocytotic cells and the total IgM concentration correlated positively with the proportion of dead *R. campanula* parasites. The result suggests that those measures of immune function may really reveal immunocompetence in roach, i.e. they indicate ability of roach to eliminate parasites, at least the prevalent tissue-dwelling digenean gill-parasite, *R. campanula*.

28-11 Talk

NESTLING IMMUNE RESPONSE TO PHYTOHAEMAGGLUTININ IS NOT HERITABLE IN COLLARED FLYCATCHERS

Natalia Pitala [1], Lars Gustafsson [2], Joanna Sendecka [2], Jon E. Brommer [1]

[1] *University of Helsinki, Department of Biological and Environmental Sciences, P.O. Box 65 (Viikinkaari 1), 00014, Helsinki, Finland*
[2] *Uppsala University, Department of Animal Ecology, Norbyvägen 18 D, 752 36, Uppsala, Sweden*

natalia.pitala@helsinki.fi

The response to intradermally injected phytohaemagglutinin (PHA-response) is a commonly used index of immunocompetence (the ability to resist pathogens) in avian studies. Parasite-mediated sexual selection requires heritable immunocompetence and PHA-response has been often studied in the context of sexual selection. Several previous studies reported heritability of PHA-response in wild bird populations. However, the evidence for heritability of PHA-response in birds largely stems from full-sib comparisons, which cannot separate non-additive genetic effects and maternal effects from additive genetic variance. Using an animal model approach, we quantified the narrow-sense heritability of PHA-response in 1,626 collared flycatcher (*Ficedula albicollis*) nestlings from 332 families; to increase the power of the analysis most of the broods were cross-fostered. Nestling PHA-response was not significantly heritable ($h^2 = 0.06 \pm 0.10$), but was subjected to non-heritable nest-of-origin effects (10% of variation). Our findings reveal a limited role of nestling PHA-response in sexual selection in the studied population and illustrate that full-sib comparisons of immunological measures may lead to inflated estimates of heritability.

28-12 Talk

SOCIAL PROPHYLAXIS: COLLECTIVE IMMUNITY IN ANT SOCIETIES

Sylvia Cremer [1], Line V. Ugelvig [1]

[1] *University of Regensburg, Biology I, Universitaetsstrasse 31, 93053, Regensburg, Germany*

sylvia.cremer@biologie.uni-regensburg.de

Group living increases the risk of parasite transmission between individuals due to frequent social contacts and a typically high genetic similarity. Prophylactic defences that prevent the spread of parasites between group members are therefore expected to have evolved in large societies, such as the colonies of social insects.

We infected a single ant worker of the invasive garden ant, *Lasius neglectus,* by applying spores of the fungus *Metarhizium anisopliae* on its cuticle, and observed the behavioural and physiological responses of naïve nestmates to this individual. We found that prophylactic hygienic behaviours were performed with a higher frequency in these groups than in controls containing only uninfected individuals. We further detected a survival benefit of ants that lived together with an infected individual when later challenged themselves with the same fungal pathogen. Potential underlying mechanisms of this 'social vaccination', which similarly occurs in termites (Traniello et al. 2002 PNAS), and the generality of this phenomenon in social insects are discussed.

28-13 Talk

SLEEP AND THE MAMMALIAN IMMUNE SYSTEM

Brian T. Preston [1], Isabella Capellini [2], Patrick McNamara [3], Robert A. Barton [2], Charles L. Nunn [1]

[1] *Max Planck Institute for Evolutionary Anthropology, Primatology, Deutscher Platz 6, 04103, Leipzig, Germany*
[2] *Durham University, Anthropology, DH1 3HN, Durham, U.K.*
[3] *Boston VA Medical Centre and Boston University School of Medicine, Department of Neurology, MA 02130, Boston, U.S.A.*

brian.preston@eva.mpg.de

Many mammals spend the majority of their lives asleep, yet the adaptive value of sleeping remains obscure. It is commonly thought that sleep is required for resisting and combating infection, but isolating an immunological benefit of sleep using diseased or sleep deprived subjects has not been possible. Here, we exploit the natural variation in sleeping times found across 26 mammalian species to investigate the evolutionary relationship between sleep and investment in immune defence. Using phylogenetic methods, we show that species that sleep for longer have greater overall numbers of circulating white blood cells, and that evolutionary increases in sleeping times are associated with investment in 4 of the 5 major immune cell types. In marked contrast with current ideas, this apparent influence of sleep was not restricted to periods of down-regulated brain function and body temperature (NREM sleep), but was also evident with increases in the 'active' phase of sleep (REM sleep). We propose that the mechanism underlying this relationship involves the costliness of maintaining an effective immune system. Our results strengthen concerns over declining sleep durations in humans, and identify sleep as a novel cost of parasite resistance.

28-14 Talk

IMMUNE DEFENCE, PATHOGENESIS AND SOME UNSETTLED QUESTIONS

Paul Schmid-Hempel [1]

[1] *ETH Zurich, Institute of Integrative Biology (IBZ), Universitätsstrasse 16, CH-8092, Zurich, Switzerland*

psh@env.ethz.ch

Immune defence is the major tool to combat parasitic infections and its variation has evolved in relation to the ecological conditions the host organism typically finds itself in. Studies done over the recent decade have accumulated evidence of the costs to the host associated with mounting or evolving an immune response, of the relationships with life history or prophylaxis strategies. Furthermore, theoretical advances have gradually started to understand the patterns from a functional point of view. However, a number of questions have remained unsettled and have not been answered in a satisfactory manner. Here, the host-parasite interaction is analysed from the point of view of the parasite's actions. A framework will be suggested to understand at least some of these unresolved question.

28-01 Poster

TRANS-GENERATIONAL COSTS OF INFECTION FOR THE MOSQUITO AEDES AEGYPTI

Philip Agnew [1], Pierre Echaubard [1, 2], Christine Sidobre [1], Ana Rivero [1, 3], Sylvain Gandon [1], Yannis Michalakis [1]

[1] *Génétique et Evolution des Maladies Infectieuses, CNRS/IRD UMR 2724, 911 Av. Agropolis, 34394, Montpellier, France*
[2] *Institut fur Integrative Biologie, ETH-Z, Universitatstrasse 16, 8092, Zurich, Switzerland*
[3] *Museo Nacional de Ciencias Naturales (CSIC), C/José Gutierrez Abascale 2, 28006, Madrid, Spain*

agnew@mpl.ird.fr

Acquired immunity is now known for several invertebrates in that it has been shown an initial challenge to an individual's immune system can stimulate a response making a secondary challenge less costly. These responses can be expressed by the same individual or their offspring. I will present the results of an experiment where the opposite was found: mosquito larvae experienced greater costs of infection if their parents had been infected by the same parasite.

28-02 Poster

DEVELOPMENTAL RATE AND IMMUNE DEFENSE IN TROPICAL AND TEMPERATE BIRDS: A COMPARATIVE FIELD STUDY

Elena Arriero [1, 2], Thomas E. Martin [2]

[1] *CNRS UMR 7103, Universite Pierre et Marie Curie, Laboratoire de Parasitologie Evolutive, 7 quai St. Bernard, Case 237, Bat A, Fr-75252, Paris cedex 05, France*
[2] *University of Montana, Montana Cooperative Wildlife Research Unit, 205 Natural Science Bldg., MT-59812, Missoula (Montana), USA*

elena.arriero@snv.jussieu.fr

Developmental rate is one of the traits that literally defines the slow-fast gradient of variation in life history strategies, but has traditionally received little attention. Slow development is thought to enhance offspring quality allowing a better development of internal components such as immune function, which may enhance adult survival. However, evidences of a relationship between immune defense and developmental periods or other life history traits are still scarce and equivocal. The variation in slow-fast life history strategies is strongly expressed geographically, with tropical species representing the "slow strategy", and north temperate species representing the "fast strategy". To address these physiology-life history relationships, we measured two indices of immune defense in nestlings of several tropical and north temperate passerine species showing an extensive variation in incubation period. As a measure of constitutive innate humoral immunity we assessed natural antibody levels, while acquired cell-mediated immunity was assessed by the broadly used PHA-skin test. Our study provides novel data on a set of phylogenetically matched species from North and South America that will offer new insights into the study of latitudinal variation in life history strategies and immune defense.

28-03 Poster

FIELD CRICKETS REALLOCATE IMMUNE EFFORT WHEN INFESTED WITH MOBILE PARASITOID LARVAE

Nathan W. Bailey [1], Marlene Zuk [1]

[1] *University of California, Riverside, Biology, Spieth Hall, 92521, Riverside, CA, USA*

nathanb@ucr.edu

The field cricket *Teleogryllus oceanicus* is attacked by an acoustically-orienting parasitoid fly, *Ormia ochracea*, where their ranges overlap in Hawaii. Fly larvae begin development in the thoracic cavity of parasitized crickets and eventually move to the abdomen, where they construct a melanized respiratory funnel to the outside using the host encapsulation response. These highly mobile larvae can thus evade initial encapsulation. Prior work has shown that crickets in heavily parasitized populations have decreased encapsulation abilities, suggesting that they may destroy larvae by disrupting the construction of the critical respiratory funnel. I used a series of artificial infestation experiments to explore how male field crickets respond immunologically to infestation by mobile parasitoid larvae. Encapsulation ability decreased and PO activity increased in both infested crickets and controls, whereas lysozyme activity decreased in infested crickets but remained constant in controls. Infested hosts harboring fewer established larvae showed greater decreases in encapsulation. Phenoloxidase activity was positively associated with the degree of larval respiratory funnel melanization, suggesting that *O. ochracea* larvae marshal immunological components produced by their hosts. These results are consistent with a trade-off within the immune system of infested hosts, and decreased encapsulation ability during late larval infestation may provide crickets in heavily parasitized populations with an unusual selective advantage.

28-04 Poster

ADAPTIVE EVOLUTION OF THE AVIAN MX GENE IMPLICATED IN THE RESISTANCE AGAINST AVIAN INFLUENZA VIRUS

Sofia Berlin [1], Qu Lujiang [1], Xian Yao Li [2], Ning Yang [2], Hans Ellegren [1]

[1] *Uppsala University, Department of Evolutionary Biology, Norbyvagen 18 D, Uppsala, Sweden*
[2] *China Agricultural University, College of Animal Science and Technology, State Key Laboratory for Agro Biotechnology, Beijing, China*

sofia.berlin@ebc.uu.se

Mx proteins are interferon-induced GTPases that confer antiviral activities against RNA viruses. In domestic chicken, allelic variants of Mx are associated with resistance against avian influenza A virus of the highly pathogenic H5N1 strain. We analysed the molecular evolution of the *Mx* gene in birds using data on interspecific divergence in anseriform and galliform birds, and on intraspecific diversity in domestic chicken populations. The overall ratio of non-synonymous to synonymous substitution was unusually high, 0.80, indicating relaxed constraint or adaptive evolution. Evidence for the latter was provided by that a total of 11-18 codons were found to have evolved under positive selection. The great majority of these codons are located in a region unique to birds at the N-terminal end of the Mx protein. Chicken polymorphism showed an excess of derived high frequency variants, which signifies recent or on-going episodes of positive selection. In sharp contrast to the strong adaptive evolution of the *Mx* gene in birds, a similar analysis of mammalian *Mx* genes failed to find evidence for positively selected codons. We hypothesize that the signatures of positive selection in the avian-specific region of the *Mx* gene could result from a host-pathogen co-evolutionary arms race or from an evolutionary history of antagonistic exposure to varied RNA viruses.

28-05 Poster

DIVERSIFICATION OF LYSOZYMES IN CAENORHABDITIS ELEGANS

Claudia M. L. Boehnisch [1], Daniel Wong [2], Kerstin Isermann [3], Thomas Roeder [3], Jonathan Ewbank [2], Nico Michiels [1], Hinrich Schulenburg [1]

[1] *University of Tuebingen, Animal Evolutionary Ecology, Auf der Morgenstelle 28, 72076, Tuebingen, Germany*
[2] *Centre d'Immunologie de Marseille Luminy, Campus de Luminy - Case 906, 13288, Marseille cedex 9, France*
[3] *University of Kiel, Zoophysiology, Am Botanischen Garten 1-9, 24188, Kiel, Germany*

claudia_boehnisch@web.de

All organisms have to adapt to heterogeneous environments like changing pathogen and food conditions in order to survive. Two outcomes of such selective pressure is the evolution of the digestion and the immune system. Interestingly lysozymes may serve both digestive and immune function with a certain degree of specificity. These enzymes originated independently in the animal kingdom. The genome of *C. elegans* encodes a comparatively large number of at least 10 different lysozymes. Phylogenetic analyses demonstrated intragenomic diversification by gene duplication and the action of positive Darwinian selection. Some of these lysozymes are known to be part of the innate immune response in the nematode. However, so far nothing is known about their digestive function in *C. elegans*. In our study we are testing whether genetic diversification translates into functional diversification resulting in groups of lysozymes either involved in digestion or immunity within *C. elegans*. We already obtained support for this hypothesis from our analysis of gene expression after exposure to food or pathogenic microbes. We also present the first results of our functional analyses using single-lysozyme knockout mutants. The *C. elegans* lysozymes may represent a typical example of evolution by gene duplication.

28-06 Poster

IMMUNO-REDISTRIUTION OVER THE ANNUAL CYCLE IN RED KNOTS (CALIDRIS CANUTUS)

Deborah M. Buehler [1], Irene Tieleman [1], Theunis Piersma [1]

[1] *University of Groningen, Animal Ecology, Kerklaan 30, 9750 AA, Haren, Netherlands*

d.m.buehler@rug.nl

The immune system is important for survival and has been increasingly measured as a proxy for self-maintenance when addressing ecological and evolutionary questions about life history. Yet very little is know about how immune function changes throughout the annual cycle. In this study we examined immune function in the context of the entire annual cycle using data taken on a monthly basis for several measures of standing (non-specific, non-induced) immune function (microbial killing, white blood cell concentrations and hemolysis-hemagglutination titers) in captive red knots (*Calidris canutus*). We further examined the effect of increased cost of living on immune function by manipulating ambient temperature to vary thermoregulation costs. To examine relationships among immune measures we performed principal component analysis (PCA). We found that annual cycle stage and acclimation to captivity affected immune function much more than our temperature manipulations. Furthermore, different measures of immune function show different patterns over the annual cycle. Within individuals, lymphocytes, monocytes and thrombocytes formed a component that we interpret as “low cost”, whereas phagocytosis-based microbial killing, heterophils and hemolysis formed a component which we interpret as “high cost”. Over the annual cycle these components indicate that during mass gain there is a shift towards higher “high cost” scores, during mass loss scores are high on both axes, and during peak moult there is a shift towards more “low cost” and less “high cost” immunity. We propose that these findings support the possibility of different immune strategies during different periods in the annual cycle via changes in investment within the standing immune system.

28-07 Poster

POST-MATING IMMUNE REGULATION IN WOOD ANTS

Gregoire Castella [1], Philippe Christe [1], Michel Chapuisat [1]

[1] *University of Lausanne, Department of Ecology and Evolution, Dorigny, 1015, Lausanne, Switzerland*

gregoire.castella@unil.ch

In ants, mating is a once in a life-time event. Ant queens mate early in adult life and store the sperm for several years, whereas males quickly die after mating. Mating and the storage of alien sperm are likely to be costly. In particular, mating might affect immune defenses. The newly mated queens have to maintain an optimal immune level in order to keep an efficient defense against pathogens (including those introduced by mating) without jeopardizing the long-term survival of sperm. Here we investigated the effects of mating on immunity by comparing the immune defenses of virgin and newly-mated wood ant (*F. paralugubris*) queens. We measured two humoral immune components: the antibacterial activity, an induced response, and the phenoloxidase activity, a constitutive defense. First, we demonstrate that mating induces a significant increase in antibacterial activity over time. This may result from the introduction of microbes in the female genital tract during mating. We then show that mating causes a short-term drop-off in phenoloxidase activity. This difference is however transient and lasts only for 7 days. Together, those results indicate that mating and long-term sperm storage may come with a cost to ant queens. They also suggest that the differential regulation of specific and general immune pathways may help queens to resolve the conflict between long-term sperm storage and efficient immune defenses.

28-08 Poster

IS THERE A ROLE FOR ANTIOXIDANT CAROTENOIDS IN LIMITING SELF-HARMING IMMUNE RESPONSE IN INVERTEBRATES?

Stéphane Cornet [1], Clotilde Biard [1], Yannick Moret [1]

[1] *Université de Bourgogne, UMR CNRS 5561 Biogéosciences, Ecologie Evolutive, 6 Bd Gabriel, 21000, Dijon, France*

stephane.cornet@u-bourgogne.fr

Deployment of an immune response is now known to be costly because of two reasons. First, it suddenly mobilises nutrients and energy that will default other important functions. Second it produces cytotoxic molecules, which not only help to kill invading pathogens but also generate damages to the host tissues along a phenomenon called self-reactivity. In arthropods, self-reactivity is believed to result from the induction of the phenoloxidase (PO) activity generating numerous reactive intermediates of oxygen and nitrogen during melanogenesis. Crustaceans possess the characteristic to store important quantities of carotenoids in their tissues and haemolymph for reasons that are yet not known. A matter of fact is that carotenoids are powerful antioxidants that are involved in the regulation of oxidative stress. Here we make the hypothesis that such an accumulation of caraotenoids in crustacean tissues may help to minimize the cost of the immune response associated with self-reactivity through scavenging free radicals and cytotoxic molecules. We consequently predict that, in natural population of crustaceans, a positive relationship between PO enzyme activity and the concentration of carotenoid in their haemolymph should exist at both individual and population levels. In a study that investigated such relationships in natural populations of the amphipod crustacean, *Gammarus pulex*, we indeed found a positive correlation between activity of the prophenoloxidase system and carotenoid contents of the haemolymph suggesting a protective role of carotenoids to oxidative damage generated by sel-reactivity.

28-09 Poster

AGE-RELATED STRATEGIES OF RESOURCE ALLOCATION TO REPRODUCTION AND IMMUNE FUNCTION IN BLUE TIT FEMALES

Anna Dubiec [1], Mariusz Cichoń [2]

[1] *Polish Academy of Sciences, Institute for Ornithology, Nadwiślańska 108, 80-680, Gdańsk, Poland*
[2] *Jagiellonian University, Institute of Environmental Sciences, Gronostajowa 7, 30-387, Kraków, Poland*

adubiec@stornit.gda.pl

Life history theory posits that age-dependent increase in fecundity may be generated by decrease in the amount of resources allocated to self-maintenance in favour of investments in reproduction. To test the hypothesis that young and older individuals differ in the strategy of resource allocation to reproduction and self-maintenance functions, the study on blue tit females was conducted. To test how young and older females respond to the increased reproductive effort some broods were enlarged while the others were left unmanipulated, and within each treatment nests were paired according to female age: a 1-year-old female and an older female. The investment in self-maintenance was assessed as the level of humoral immune response, and investment in reproduction as nestling condition reflected by body mass, tarsus length and the level of T-cell-mediated immune response. Our main interest was the interaction between age and brood size treatment as we expected that young and older females should differently respond to the increased reproductive effort. Brood size enlargement resulted in decreased nestling body mass, tarsus length and cell-mediated immunity, however it had no effect on immune responsiveness in females. Young and older females did not differ neither in nestling condition nor their humoral response. Given the lack of interaction between brood size treatment and female age both in the analyses of female humoral immune response and nestling condition, one may conclude that in blue tits, young and older females do not differ in their patterns of resources allocation to reproduction and immune function.

28-10 Poster

EFFECT OF FOOD LIMITATION ON STANDING IMMUNITY AND THE SICKNESS RESPONSE IN RED KNOTS (CALIDRIS CANUTUS)

Francisco A. Encinas-Viso [1], Deborah M. Buehler [1], Magali Petit [2, 3], B. Irene Tieleman [1], Theunis Piersma [1, 3]

[1] *University of Groningen, Animal Ecology Group, Kerklaan 30, 9751 NN, Haren, The Netherlands*
[2] *University Pierre et Marie Curie, Paris, France*
[3] *Royal Netherlands Institute for Sea Research (NIOZ), Landsdiep 4, 1797 SZ, Texel, The Netherlands*

f.a.encinas.viso@student.rug.nl

Resources are important in the maintenance and mounting of an immune response. The implied costs of immunity is one of the assumptions behind the idea that immunity may be traded-off in favour of other demanding activities (migration, reproduction) when resource are scarce and also traded-off with maintenance of body condition. To examine this we manipulated food availability for Red Knots (Calidris canutus islandica), a long-distance migrant shorebird, to see how knots balance conflicting physiological demands when faced with a limited energy supply. We predicted that food limitation would have a negative effect on immunity; however, since different “stessors” can have differing effects on different parts on the immune system and because different parts of the system have different costs, simple “higher versus lower” predictions were not possible. We measured standing innate immunity using several techniques: including white blood cell counts (WBC), Haemolysis- haemaggluttination (HL-HA), microbial killing and haptoglobin. We also measured body condition using body mass and haematocrit. Finally, we induced a sickness response with an LPS injection and measured the intensity of the response by examining body mass temperature and behaviour. The results indicated that birds under food-limitation showed reduced body mass, low haematocrit and changes in immune function. Also birds under food limitation and LPS injection had fever, and all birds injected with LPS showed lower haematocrit and a tendency for higher bacterial killing. We conclude that resource availability affects both body condition and innate immune response in red knots.

28-11 Poster

IMMUNE FUNCTION IS ASSOCIATED WITH LOCAL EFFECT HETEROZYGOSITY IN BLUETHROAT NESTLINGS

Frode Fossøy [1], Arild Johnsen [1], Jan T. Lifjeld [1]

[1] *University of Oslo, Natural History Museum, P.O. Box 1172 Blindern, 0318, Oslo, Norway*

frode.fossoy@nhm.uio.no

Immune function has previously been found to be related to the level of inbreeding or genetic diversity. A common approach for estimating genetic diversity is the use of several neutral microsatellite markers to calculate multilocus heterozygosity, assuming that it reflects the genome-wide level of genetic diversity. In bluethroat nestlings, we found that significant associations between PHA response and two different measures of microsatellite heterozygosity, i.e. individual heterozygosity and mean d2, could be explained by two different single loci effects, suggesting a local effect of heterozygosity. Hence, the PHA response in bluethroat nestlings is more likely associated with the heterozygosity of certain functional genes rather than genome-wide heterozygosity.

28-12 Poster

IMMUNE SYSTEM INDUCTION AND FITNESS COSTS OF BACTERIAL CONSUMPTION IN AN INSECT HERBIVORE (TRICHOPLUSIA NI, LEPIDOPTERA)

Dalial Freitak [1], Chris W. Wheat [2], David G. Heckel [1], Heiko Vogel [1]

[1] *Max Planck Institute for Chemical Ecology, Entomology, Germany, Jena, Hans Knoell 8, 07745*
[2] *University of Helsinki, Biological and Environmental Sciences, FI-00014, Helsinki, Finland*

dfreitak@ice.mpg.de

Insects are known to possess only innate immune responses. Nevertheless immune recognition is highly specific and insects are able to differentiate between great numbers of immune elicitors coming from a variety of pathogens. It has been argued that costs for immune defense, tolerance and resistance vary under different environmental conditions, depending among others on the occurrence and density of possible pathogens.

Herbivorous insects, such as lepidopteran larvae consume vast amounts of plant material in the course of their life span. Plant surfaces are often covered with large numbers of microorganisms, some of which are potentially pathogenic. Here, we examine the consequences of exposing an agricultural insect pest to non-infectious microorganisms via simple oral consumption. The consequences of ingesting non-pathogenic bacteria can be observed on three different levels – enzymatic activities and protein expression in hemolymph accompanied by the up regulation of immunity related gene expression in the midgut tissue. In addition, we also observed a strong effect of bacterial diet on fitness related traits of the insects. A possible immune priming due to parental effects was also examined by investigating the immunity related traits in the larvae of the next generation.

In the current experiment we clearly demonstrate that *T. ni* larvae are able to detect and respond to microbes encountered through the food, likely using midgut epithelial tissue as a sensing organ. These results strongly suggest that food plant microbial communities may represent a dynamic and unstudied part of the evolutionary interactions between plants and their insect herbivores.

28-13 Poster

A ROLE OF BLOOD PARASITES FOR MAINTAINING ADDITIVE GENETIC VARIANCE OF FITNESS IN COLLARED FLYCATCHERS

Lars Gustafsson [1]

[1] *Uppsala Univeristy, Ecology & Evolution, Animal Ecology, Norbyvägen 18D, SE-752 36, Uppsala, Sweden*

lars.gustafsson@ebc.uu.se

One of the most debated questions in evolutionary biology is how additive genetic variance of female and males fitness can be maintained in natural populations near equilibrium. To date, empirical studies have provided support for parts of this scenario by using animal-model quantitative genetic analysis on data from over 8,500 collared flycatchers (Ficedula albicollis) in a population followed for 25 years. Additive genetic variance for fitness measured as annual fitness and lifetime reproductive success was low but positive and significantly different from zero. I will here explore the role of blood parasites and changing climate, in two different periods ten years apart for individual fitness and parent offspring resemblance in fitness. The relative negative effect of some blood parasites species differed between the time periods as did their association with a sexually selected trait that is also related to climate change. Yearly climate interacted with parent offspring resemblance in fitness. A possible role for changing host immune function and parasite prevalence in a changing climate in maintaining additive genetic variance of female and males fitness will be discussed.

28-14 Poster

GREATER EXPOSURE TO PARASITES AND INCREASED DISEASE RESISTANCE IN AN AVIAN BROOD PARASITE

Caldwell Hahn [1]

[1] *USGS-Patuxent Wildlife Research Center, Laurel, MD, US*

hahn@psychology.rutgers.edu

We hypothesized that avian brood parasites have evolved greater disease resistance as a result of increased exposure to parasites. Female brood parasites lay their eggs in other species' nests, where they are exposed to their ectoparasites. Young brood parasites are more extensively exposed to parasites, because they hatch in foster parents' nests, where they are physically brooded, then fed by mouth for several weeks until they are independent. We tested our hypothesis on the North American brood parasite, the brown-headed cowbird (*Molothrus ater,* Icteridae). This cowbird is exposed to a particularly wide array of other species' parasites, because across its geographic range, cowbirds lay their eggs in the nests of over 200 different songbird species. We examined whether cowbirds are exposed to more parasites by quantifying the ectoparasites found on cowbirds and on the non-parasitic Passerines they parasitize. We found that brown-headed cowbirds were infected by a significantly greater diversity of lice than the non-parasitic songbirds. Next we examined the cowbird's disease resistance in an experimental infection study using three arboviruses that cause significant disease and mortality in birds, West Nile virus, Western equine encephalomyelitis virus, and St. Louis encephalitis virus. We experimentally infected cowbirds and three related, non-parasitic Icterid species and compared immune responses. The cowbirds were significantly more disease resistant to all three viruses than their non-parasitic relatives using multiple parameters. Cowbirds showed no mortality, a lower proportion of infected birds, lower level of viremia when infected as well as shorter time to recovery. Cowbirds also appeared to use different immune mechanisms in response to these infections, because they had lower levels of antibodies than the other species. We discuss the life history trade-offs that may be associated with increased disease resistance in cowbirds.

28-15 Poster

COSTS OF IMMUNITY OR ADAPTIVE LIFE HISTORY DESICIONS?

Sveinn Are Hanssen [1]

[1] *Norwegian Institute for Nature Research, dept of arctic ecology, Polar Environmental Centre, 9296, Tromsø, Norway*

sveinnare@gmail.com

An induced immune challenge may have two counteracting effects on an individual's reproductive investment. (i) The resource demand may increase to "fuel" the immunologic reaction, which in turn may lead to an adaptive *decrease* in investment in resource-costly activities such as reproduction. One the other hand, (ii) the individual may assume that the immune activity it experiences is indicative of a serious infection. The latter may lead to an adaptive *increase* in reproductive investment in response to the reduced prospects of survival and future reproduction, so called "terminal investment". In order to measure such life-history related consequences of increased immune activity, one group of incubating female common eiders *Somateria mollissima* was injected with a non-pathogenic antigen (sheep red blood cells, SRBC) while controls were injected with sterile saline. The eider is a long-lived sea-duck where females, who incubate the eggs and care for young without assistance from the male, engage in facultative anorexia during incubation leading to a large reduction in body mass. Eiders may abandon their young to other females at the cost of reduced young survival. The immune challenge resulted in a larger mass loss, a prolonged incubation period and reduced return rate, demonstrating both short- and long-term costs of immune challenge. Additionally, in response to what may have been interpreted as reduced survival chances in immune challenged females, these females more often tended their own brood after hatching, despite having suffered higher costs during incubation.

28-16 Poster

IMMUNE DEFENCE ABILITY AND PARASITE ABUNDANCE IN A DAMSELFLY, COENAGRION ARMATUM

Johanna Honkavaara [1], Jukka Suhonen [1], Markus J. Rantala [1]

[1] *University of Turku, Department of Biology, Section of Ecology, 20014, Turku, Finland*

johhon@utu.fi

Parasite resistance and mating may both incur substantial costs, and there might be a trade-off between these functions. In previous studies with damselflies, parasite load has been negatively correlated with mating success, male condition and longevity. We studied on *Coenagrion armatum* if natural ecto- and endoparasite infection levels affect males' ability to further mount an immune response and if there is a difference between mated and single males in this response in two separate populations. We also measured encapsulation response (with inserted nylon monofilament) of mated and single males. There were no population differences in any morphological or immunological measurements. Most damselflies (78%) had no mites and single males had more mites than mated males. For males without mites, mated males had lower encapsulation response than single males, whereas for infected males such a difference was not found (there were only four mated males with mites). Also, there was a tendency for mite infected single males to have lower encapsulation response than those without mites. For males with mites, encapsulation response was negatively correlated with mite abundance. Although gregarine prevalence was high (77.8%), intensity of gregarine infection was not correlated with encapsulation response. Our results indicate that males infested with mites might have less resources (f.ex. melanin) for further encapsulation response. On the other hand, high immune defence ability might explain low success of mites. However, trade-off between immunity and mating may be reflected in the lower encapsulation response of recently mated males.

28-17 Poster

OXIDATIVE STRESS AS A COST OF IMMUNE ACTIVATION. AN EXPERIMENT WITH GREENFINCHES.

Peeter Hõrak [1], Lauri Saks [1], Mihkel Zilmer [2], Ulvi Karu [1], Kersti Zilmer [2]

[1] Tartu University, Institute of Zoology and Hydrobiology, Vanemuise 46, 51014, Tartu, Estonia
[2] Tartu University, Department of Biochemistry, Ravila 19, 50411, Tartu, Estonia

horak@ut.ee

Reactive oxygen and nitrogen species produced by metabolism and immune defences can cause extensive damage to biomolecules. To counteract this damage, organisms rely on exogenous and endogenous antioxidants, relative importance of which in maintaining redox balance is not clear. We supplemented captive greenfinches with dietary antioxidants – carotenoids and vitamin E – and subsequently injected them with an inflammatory agent phytohemagglutinin. Compared to controls, immune challenged birds circulated more lipid peroxidation products but also increased total plasma antioxidativity. Carotenoid (but not vitamin E) supplementation reduced lipid peroxidation but this did not compensate for the effects of immune activation. Levels of an endogenous antioxidant – uric acid – strongly contributed to plasma antioxidativity, while carotenoids or vitamin E had no effect. These results demonstrate that activation of innate immune responses can invoke a cost in terms of oxidative-stress driven damages and that it can also induce a compensatory increase in antioxidant protection. Exogenous and endogenous antioxidants seem to play different roles in stimulating antioxidant protection and alleviating oxidative damages. This study also showed that simultaneous assessment of oxidative stress-driven damages, antioxidant barrier, and individual antioxidants is required for explaining the potential costs of immune activation.

28-18 Poster

PLUMAGE COLORATION IS NOT AFFECTED BY VITAMIN E SUPPLEMENTATION IN MALE GREENFINCHES

Ulvi Karu [1], Lauri Saks [1], Peeter Hõrak [1]

[1] University of Tartu, Institute of Zoology and Hydrobiology, Vanemuise 46, 51014, Tartu, Estonia

ulvika@ut.ee

Carotenoid-based colours have become an important model of honest signalling as carotenoids are suggested to play vital roles in several physiological functions including as antioxidants and immunostimulators, while also required for sexual displays. However, it has been recently suggested that carotenoid-based signals may be used mainly as reflectors of the systems (mainly the amount of other non-pigmented antioxidants) that prevent their oxidation rather than the antioxidative properties of carotenoids themselves. We tested this hypothesis by examining the effect of simultaneous supplementation of carotenoids and uncoloured antioxidant – vitamin E on the coloration of growing tail feathers in captive male greenfinches. While carotenoid supplementation enhanced the coloration of the feathers, manipulation of dietary vitamin E had no effect. Thus, our results do not support the idea that carotenoids are mainly used as indicators of abundance of other antioxidants.

28-19 Poster

EVASION OF IMMUNE SYSTEM, HOST DEVELOPMENT AND EVOLUTIONARY TRANSITION IN A EUKARYOTE-PROKARYOTE ASSOCIATION.

Natacha Kremer [1], Bart A. Pannebakker [2], Hélène Henri [1], Delphine Charif [1], Fabrice Vavre [1]

[1] Université de Lyon ; Université Lyon1 ; CNRS, Laboratoire de Biométrie et Biologie Evolutive, UMR 5558, 43, boulevard du 11 novembre 1918, F-69622, Villeurbanne Cedex, France
[2] University of Edinburgh ; Institute of Evolutionary Biology, School of Biological Sciences ; Ashworth Laboratories, King's Buildings; West Mains Road, EH9 3JT, Edinburgh, Scotland ; United Kingdom

kremer@biomserv.univ-lyon1.fr

Interactions between eukaryotes and prokaryotes imply an evasion of the eukaryotic immune system by the bacteria. Futhermore, symbiotic bacteria often induce dramatic morphogenesis of host organs such as nodules (plants) or bacteriomes (insects). Because immune genes are highly pleiotropic and are often involved in development as well, developmental modifications in symbiotic associations could originate from the manipulation of host immune system.

This is suggested in the association between the parasitoid wasp *Asobara tabida* (Hymenoptera) and the intracellular bacterium *Wolbachia* (Anaplasmastaceae). *Wolbachia* is generally facultative to its arthropod's host, but is essential for female oogenesis in *A. tabida*. The transition towards obligatory dependence is evolutionarily recent, allowing us to investigate the mechanisms underlying the establishment of this dependence. TUNEL staining showed early apoptosis of nurse cells surrounding oocytes in the ovaries of aposymbiotic females. In addition to our microscopic observations, a comparative transcriptomic approach (SSH) highlighted genes that are involved in apoptosis and tumorisation processes.

Intracellular pathogenic bacteria such as *Rickettsia* are known to manipulate host immune system by down-regulating apoptosis, and *Wolbachia* could also use a similar strategy. Apoptosis manipulation may have been secondary recruited for oogenesis control in *A. tabida*. In this way, manipulation of host immune system could explain a swift transition from parasitism to mutualism without provision of new capabilities to the host by the symbiont.

28-20 Poster

EVOLUTIONARY ASPECTS OF THE DAPHNIA MAGNA IMMUNE SYSTEM

Pierrick Labbé [1], Tom Little [2]

[1] University of Edinburgh, Institute of Evolutionary Biology, Room 415 , IEB, Ashworth Laboratory,Kings Buildings, EH9 3JU, Edinburgh, UK
[2] University of Edinburgh, Institute of Evolutionary Biology, IEB, Ashworth Laboratory,Kings Buildings, EH9 3JU, Edinburgh, UK

Pierrick.Labbe@ed.ac.uk

The mechanisms of invertebrate immunity are increasingly understood, but there remains little understanding either of how immune systems function in the real world or of the evolutionary forces that shape variability in immune effectors. Model organisms that are valuable for use in field epidemiology and evolutionary studies do of course exist, but these have not been studied in terms of immune effector mechanisms. Equally, there are cases where particular facets of the immune system have been linked to disease (e.g. human MHC), but these are typically in organisms that are not amenable to experimentation or evolutionary studies. Our work on *Daphnia* stands to reveal how immune reactions are linked to disease or immunopathology under natural settings and how variation in the strength of these reactions ultimately shapes the genetic structure and evolution of host populations. We aim to link the activity of key effectors of the invertebrate immune system to parasite resistance under natural levels of environmental and genetic variation. Using the extensively investigated *Daphnia*-parasite system, we modify the immune response of the host, study immune response variation under different ecological or genetic environments, and ultimately seek to link genetic differences to whole organism resistance phenotypes. We will present some results of this work and show how it contributes to the emerging ecological immunity field.

28-21 Poster

ANTIBODY CONCENTRATION IN EGGS OF THE ZEBRA FINCH IN RELATION TO PRIMARY AND SECONDARY IMMUNIZATION

Rafał Martyka [1], Heli Siitari [2], Mariusz Cichoń [1], Joanna Rutkowska [1]

[1] Jagiellonian University, Institute of Environmental Sciences, Gronostajowa 7, 30-387, Kraków, Poland
[2] University of Jyväskylä, Department of Biological and Environmental Sciences, PO Box 35, FI-40014, Jyväskylä, Finland

martyka@eko.uj.edu.pl

Female birds transfer antibodies through the eggs to protect newly hatched nestlings against pathogens and thus to enhance their survival prospects. We studied the effect of primary and secondary immunization of a female on the level of maternal antibodies in the eggs. Experimental females were inoculated with sheep red blood cells (SRBC) before egg laying, after laying the first egg or at both occasions, whereas control females received saline injection. Each egg was broken at the day of laying and yolk was separated from albumen. Subsequently yolk samples were analyzed in order to determine IgY concentration. We found no significant differences in the yolk IgY concentration among experimental groups. However, there was a significant interaction between experimental group and laying order which resulted from the fact that antibody concentration increased with laying sequence among females receiving secondary immunization. In all other groups the concentration of antibodies remained constant in subsequent eggs. These results suggest that maternal transfer of antibodies may be affected only by the secondary exposure to the antigen.

28-22 Poster

RAPID EVOLUTION OF A STRESS RESPONSE IN A NATURAL POPULATION OF DAPHNIA MAGNA

Kevin Pauwels [1], Robby Stoks [1], Ellen Decaestecker [1], Luc De Meester [1]

[1] KULeuven, Biology, Deberiotstraat 32, B3000 Leuven, Belgium

Kevin.Pauwels@bio.kuleuven.be

Populations often face changes in environmental conditions at a relatively short timescale, which may lead to micro-evolution of traits to cope with these changing selective pressures. Here, we demonstrate micro-evolution of a physiological trait in a natural population of the water flea *Daphnia magna*. Levels of the stress protein Hsp60 showed genetic variation, indicating in situ evolutionary potential, and increased through time. The observed micro-evolutionary increase did not fit the historically documented changes in fish predation pressure in this pond, but paralleled an increase in load of infective stages of epibionts through time. In line with this, the locally most abundant epibiont caused an induction of Hsp60. As stress proteins show evolutionary potential and protect organisms against a wide array of environmental factors, micro-evolution of stress proteins in natural populations is likely to be common.

28-23 Poster

INBREEDING AND EXTREME OUTBREEDING CAUSES SEX DIFFERENCES IN IMMUNE DEFENCE AND LIFE HISTORY TRAITS IN EPIRRITA AUTUMNATA

Markus J. Rantala [1], Derek A. Roff [2]

[1] *University of Turku, Department of Biology, Section of Ecology, FIN-20014 Turku, Finland*
[2] *University of California, Riverside, Department of Biology, Riverside, CA 92521, USA*

markus.rantala@utu.fi

Empirical studies in vertebrates support the hypothesis that inbreeding reduces resistance against parasites and pathogens. However, studies in insects have not found any evidence that inbreeding compromises immune defence. Here we tested whether one generation of brother-sister mating or extreme outbreeding (mating between two populations) have an effect on innate immunity and life history traits in the autumnal moth, *Epirrita autumnata*. We show that the effect of inbreeding on immune response differed between the sexes: while in females, inbreeding significantly reduced encapsulation response against nylon monofilament ability, it did not have a significant effect on male immune response. There were also differences in the correlation of the immune response with other traits: in females increased immune response was positively correlated with large size, whereas in males immune response increased with a reduction in development time. Immune response differed significantly among families in males but not in females, both for the inbreeding and extreme outbreeding experiments. In conjuction with the observed immune responses to inbreeding, these data suggest that in males genetic variation for immune response is largely additive or non-directional with respect to dominance, whereas in females variation is much reduced and consists of directional dominance variance. We show that encapsulation response against nylon monofilament is associated with the resistance against real pathogens suggesting that this widely used method to measure the strength of immune defence in insects is also a biologically relevant method.

28-24 Poster

INVESTIGATING THE MOLECULAR BASIS OF IMMUNE SPECIFICITY IN THE BUMBLEBEE/CRITHIDIA HOST-PARASITE SYSTEM

Carolyn E. Riddell [1], Eamonn B. Mallon [1]

[1] *University of Leicester, Biology, University Road, LE1 7RH, Leicester, UK*

cr63@le.ac.uk

The complex processes underlying immunity include some components, such as antibodies, that are highly specific to particular infectious agents, and others that are generally considered non-specific. Invertebrate animals like insects do not possess antibodies, and their immune systems have generally been considered to rely solely on non-specific mechanisms. There is, however, ecological evidence that there may be other, as yet unidentified, mechanisms of specific immunity. Invertebrates respond to individual pathogen species or strains with varying degrees of specificity proving that, though lacking T-cell proliferation and antibody production, invertebrate innate immunity can similarly adapt to prevailing pathogen exposures that are constantly evolving and diversifying. Innate immunity's capabilities extend beyond a basic general response to any pathogen insult. Currently, the mechanism(s) of specificity remains an enigma, limiting our ability to understand how specificity is regulated by pathogen exposure and, consequently, how it might evolve. My research is investigating specificity in the Bombus (bumblebee)/Crithidia host-parasite system. Using subtractive suppressive hybridisation (SSH) I am identifying immune genes differentially expressed in the bumblebee in response to a Crithidia infection. Subsequently, the expression of these genes will be analysed in response to different Crithidia strains, and by correlating to the infection intensities of each colony-strain interaction, will begin to identify genes involved in immune specificity.

28-25 Poster

LONGTERM EFFECTS OF YOLK STEROIDS AND NEONATAL DIET ON ADULT IMMUNITY IN ZEBRA FINCHES.

Maria I. Sandell [1], Tobler Michael [1]

[1] *Lund University, Dept of Animal Ecology, Ecology Building, 223 62, Lund, Sweden*

Maria.Sandell@zooekol.lu.se

Maternal effects during both embryonic and offspring rearing phase modulate a multitude of morphological and physiological traits in the offspring of many vertebrate species. We tested whether prenatal androgen exposure or neonatal carotenoid diet exposure can have long-lasting effects on humoral immunity and bill colour in the zebra finch (*Taeniopygia guttata*). Egg testosterone negatively affected humoral immune responsiveness in adult zebra finches and supplementation of carotenoids during the early nestling phase also influenced immune response during the adult stage. We also found unexpected interactions between yolk testosterone and carotenoid supplementation suggesting synergistic effects of egg components and rearing environment.

28-26 Poster

IMPORTANCE OF THE ECOLOGICAL CONTEXT FOR IMMUNO-ECOLOGY STUDIES: ILLUSTRATION WITH THE SEABIRD-TICK-BORRELIA SYSTEM

Vincent Staszewski [1], Karen D. McCoy [2], Torkild Tveraa [3], Thierry Boulinier [4]

[1] *Department of Biological and Environmental Science, FIN-40014, JYVASKYLA, FINLAND*
[2] *CNRS/IRD, Génétique et Evolution des Maladies Infectieuses, UMR 2724, 34000, MONTPELLIER, FRANCE*
[3] *N.I.N.A., Polarmiljøsenteret, NO-9296, TROMSO, NORWAY*
[4] *CEFE-CNRS, Ecologie Spatiale des Populations, 1919 route de Mende, 34000, MONTPELLIER, FRANCE*

vincent.staszewski@snv.jussieu.fr

One goal of the evolutionary ecology approach of immunocompetence is to explain why inter-individual variation exists despite the obvious fitness benefits of resistance against parasites. To address this topic, experimental exposure to artificial antigens has been used to investigate fitness costs associated to the development of an immune response. Unfortunately, this can lead one to neglect the ecological context of host exposure to parasitism.

In a host-parasite system involving seabirds, the bacterium *Borrelia burgdorferi* sensu lato, and its tick vector *Ixodes uriae*, the long-lived vertebrate species are exposed every breeding season to a parasite pressure that is spatially heterogeneous, but repeatable in time. This provides an ideal framework to study the immune response as an induced response to environmental pressure. Here, we test the effect of spatio-temporal variability of parasitism on antibodies (Ab) levels at an interindividual level and for species with different patterns of exposure. Our results show that the immunological profiles (i.e. quantity and repertoire of anti-*Borrelia* Ab) are highly repeatable among years. We nevertheless also observed that residual year-to-year changes of Ab levels can be related to tick exposure the previous year. Similarly, we have shown that the prevalence of individuals with Ab against *Borrelia* and the repertoire of anti-*Borrelia* Ab can vary among seabird host species and colonies within the North Atlantic. Host-specific races in the tick vector and differences in the life history characteristics of the hosts may explain these results. Ecological factors likely to affect exposure risk and the response to parasitism will ultimately affect the evolution of host parasite interactions.

28-27 Poster

EVOLUTIONARY CONSEQUENCES OF DIFFERENTIAL INVESTMENT IN IMMUNE DEFENCE FOR BOTH HOSTS AND THEIR PARASITES

Barbara Tschirren [1, 2]

[1] *University of New South Wales, School of Biological, Earth and Environmental Sciences, Kensington, 2052, Sydney, Australia*
[2] *University of Bern, Evolutionary Ecology Group, Baltzerstrasse 6, 3012, Bern, Switzerland*

barbara.tschirren@unsw.edu.au

The evolution of optimal functioning and maintenance of the immune system is thought to be driven by the host's costs arising from the allocation of resources to immune functions rather than to growth and reproduction, and by the benefits arising from a better defence if an infection occurs. In young animals there is a high premium for fast growth and competitiveness, and a trade-off is thus predicted between the allocation of resources to growth versus immune function. The optimal solution for this trade-off is likely to be mediated by parasite abundance, and will significantly affect host life history, but also parasite fitness. To investigated the evolutionary consequences of differential investment in growth versus immunity, I experimentally manipulated the level of immune defence in free-living great tit nestlings by a supplementation of an immunostimulant and the abundance of their most common ectoparasite, the hen flea, to assess not only the host's costs and benefits of investing in immune defence, but also the consequences of such differential host investment strategies for parasite fitness. The results of these experiments highlight the importance of host immunity in shaping the evolutionary dynamics in host-parasite systems.

28-28 Poster

PARASITE RECOGNITION ABILITIES IN ANT SOCIETIES

Line V. Ugelvig [1, 2], Alexandra Schrempf [1], Sylvia Cremer [1]

[1] *University of Regensburg, Biology I, Universitaetsstrasse 31, 93053, Regensburg, Germany*
[2] *University of Copenhagen, Population Biology, Universitetsparken 15, 2100, Copenhagen, Denmark*

lvugelvig@bi.ku.dk

Ant societies have both behavioural and physiological defence mechanisms to prevent fatal disease outbreaks within the society. The important first barrier a parasite has to overcome to infect the society is to "enter the fortress" undetected. The efficiency of defence against parasite entrance into the colony therefore crucially depends on the ants' ability to not only recognize already sick individuals but even distinguish incoming dangerous parasites from harmless objects.

We studied groups of worker ants in the laboratory, to which we added brood treated with either (a) a control solution, (b) dead un-infectious spores, and (c) alive infectious spores of the entomopathogenic fungus *Metarhizium anisopliae*. We found that the ants can distinguish infectious spores from dead ones and increase the frequency of hygienic behaviours towards brood treated with live spores only. These hygienic behaviours were elicited almost immediately after application of the fungal spores, implying that the ants recognized the presence of the parasite rather than reacting on any signs of sickness of the brood. Furthermore, different stages of infected brood (larvae versus pupae) elicited different responses.

28-29 Poster

DOES COPULATION CORRUPT RESISTANCE AGAINST REAL PATHOGENS?

Terhi Valtonen [1], Markus J. Rantala [1]

[1] University of Turku, Biology, Turun yliopisto, 20024, Turku, Finland

terval@utu.fi

Reproduction and immunity are intimately linked to fitness. Organisms partition resources between different fitness components. Reproduction and immunity are both costly functions. In many species reproduction results in declines in other components of fitness and according to the life-history theory, costly immune functions are traded-off against other life-history components such as reproduction and growth. A growing number of papers have examined the possible trade-offs between reproduction and immunity. Here we examined whether mating affects immunity, both innate and against parasites, in mealworm beetle *Tenebrio molitor*. The results are discussed in the light of the life-history evolution.

28-30 Poster

HEAVY METALS AFFECT THE IMMUNE FUNCTION OF AN INSECT HERBIVORE EPIRRITA AUTUMNATA

Tapio van Ooik [1], Teija Ruuhola [1], Juha-Pekka Salminen [2], Markus Rantala [1]

[1] University of Turku, Section of Ecology, Department of Biology, FI-20014, Turku, Finland
[2] University of Turku, Department of Chemistry, FI-20014, Turku, Finland

tapvan@utu.fi

Heavy metals have toxic effects on plants and animals. Besides having harmful effects on invertebrate growth, pollution may have adverse effects on immune function as well. We have examined what kind of effects atmospheric pollutants have on a generalist insect herbivore *Epirrita autumnata*. We found that *E. autumnata* larvae, which were fed with leaves that came from metal polluted area, had an enhanced immune function. To investigate further for the cause of the enhanced immunity we examined experimentally the direct influence of heavy metal pollutants nickel and copper on the immune function and fecundity of the geometrid moth. We added metals to birch leaf surfaces artificially. A moderate amount of nickel and copper in the diet of moth larvae increased their encapsulation rate, but large amounts lead to inhibition of immune function. The results indicate that nickel and copper have direct effects on immunity. Additionally we found that the sex of the herbivore may play a role. Males and females reacted differently to heavy metal treatments.

28-31 Poster

IMMUNE FUNCTION, ENERGETICS AND CORTICOSTERONE LEVELS: A COMMON-GARDEN STUDY ON STONECHATS FROM DIFFERENT ENVIRONMENTS

Maaike Versteegh [1], Barbara Helm [2], Irene Tieleman [1]

[1] University of Groningen, Centre for ecology and evolutionary studies, Haren, The Netherlands
[2] Max Planck Gesellschaft, Max Planck Institute for Ornithology, Postbox 14, 9750AA, Andechs, Germany

m.a.versteegh@rug.nl

Life history traits can be phenotypically adjusted to prevailing environmental conditions but can also evolve in response to such conditions. The assembly of stonechats (*Saxicola torquata*) originating from populations with markedly different life history characteristics reared in a common garden provide excellent opportunities to study the endogenous basis for adaptations of interconnected physiological systems. The stonechat assembly maintained at the Max Planck Institute for Ornithology consists of resident equatorial birds from Kenya that have evolved in a year-round benign environment, central European birds from environments with moderate seasonal variation, and stonechats from Kazakhstan that are subjected to severe seasonality. The seasonality of the respective environments is reflected in the birds' different internal annual calendars as exemplified by their diverse migratory strategies. Winter is quiescent period for stonechats and measurements are not confounded by physiological adaptations to migration, breeding or moult. We study innate immune function by examining the bactericidal ability of blood when subjected to *Escherichia coli*, *Staphylococcus aureus* and *Candida albicans* and quantifying natural antibodies and complement in winter. In addition to measuring innate immunity, we determine basal metabolic rates of the same birds. We also determined baseline and stress induced corticosterone levels of blood plasma. Preliminary results suggest that subspecies differ in their innate immune function and energetics in winter: the long distance migrants from Kazakhstan display the highest bacteria killing ability and the highest BMR. These results tentatively support the hypothesis that animals that live in disease-prone environments or that encounter multiple different habitats should invest more in immune defense.

28-32 Poster

MOLECULAR EVOLUTION OF IMMUNE GENES IN ANTS

Lumi Viljakainen [1]

[1] University of Oulu, Department of Biology, PO Box 3000, 90014, Oulu, Finland

lumi.viljakainen@oulu.fi

An essential feature of social insects is the formation of colonies in which related individuals behave cooperatively. This, in addition to the reproductive division of labour, has made possible the evolutionary success of social insects. A major cost of social life is the higher amount of pathogens in large groups and the more likely transmission of pathogens among closely related individuals. Consequently in social insects there should be a strong selection pressure on components associated with resistance to infectious diseases. By comparing the dN/dS ratios I have investigated possible signs of selection in an antimicrobial peptide defensin from various ant species. The mature peptide consists of 40-45 amino acid sites, of which one was found to be affected by positive selection. Interestingly, the site position is in the N-terminal loop preceding the conserved CSαβ motif. The N-terminal loop has been suggested to be involved in the level of activity and antibiotic specificity of defensin. Moreover, I have identified several other putative immune genes from ants and am going to further investigate the role of natural selection in the ant innate immune system.

28-33 Poster

IMMUNE DEFENSE AND FITNESS OF ANT COLONIES

Emma Vitikainen [1], Cathy Haag-Liautard [2], Liselotte Sundström [1]

[1] University of Helsinki, Department of Biological and Environmental Sciences, P. O Box 65, FIN-00014, Helsinki, Finland
[2] University of Edinburgh, Institute of Evolutionary Biology, Ashworth Lab. 3, West Mains Rd., EH9 3JT, Edinburgh, UK

emma.vitikainen@helsinki.fi

A key challenge in ecological immunology is to understand the interplay between fitness and the immune defense of individuals. Effective allocation of resources may require trade-offs between reproduction and immune responses, or between different components of immune defense. Perennial ant colonies provide an interesting system to study these relationships.

Ants are social insects, and their colonies can harbor thousands of closely related individuals at very high densities, thus facilitating the spread of disease and parasites between colony members. Ant workers may therefore be selected for enhanced immune defense, and genetically more diverse colonies may gain advantage for having increased resistance to parasites. The life-history differences between different colony members provide another interesting aspect: while worker ants are generally short-lived, the reproductive females, queens, can live up to decades, while facing the possible trade-offs between investing in reproduction and in immune defense.

With this study we wish to elucidate how different components of immune defense interact in queen and worker ants, and how the variation in the immune response corresponds to the fitness and genetic diversity of the colonies. The study was done in a Finnish population of the ant *Formica exsecta*. We used encapsulation response and antimicrobial activity as measures of immune defense. Estimates of fitness components come from yearly surveys on the colonies, and the genetic structure of the colonies is known from previous studies. The study will give us important information on how variance in genetic diversity and immune response affects the lives of social insects in their natural environment.

28-34 Poster

YOUNG MALE MICE EXPOSED TO FEMALE ODOR GROW FASTER, BUT AT WHAT COST?

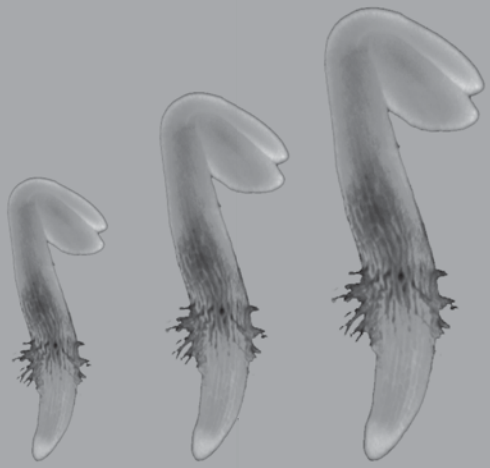
Sarah M. Zala [1, 2], Dustin J. Penn [1, 3]

[1] Austrian Academy of Sciences, Konrad Lorenz Institute for Ethology, Savoyenstrasse 1a, 1160, Vienna, Austria
[2] University of Utah, 257 S. 1400 E, 84112, Salt Lake City, USA
[3] University of Utah, Department of Biology, 257 S. 1400 E, 84112, Salt Lake City, USA

s.zala@klivv.oeaw.ac.at

It is thought that testosterone-dependent secondary sexual characters reveal a male's immunocompetence because of physiological tradeoffs between these two energetically costly traits ("immunocompetence handicap hypothesis"). If such a tradeoff exists, then experimentally increasing the expression of testosterone-dependant secondary sexual characters should result in reduced ability to resolve or cope with infection. In this study, we exposed young male mice to the odor of females, which triggers an increase in testosterone concentration and scent-marking behavior, and we monitored their growth before and after a bacterial infection, as well as their ability to resolve infection. We found no evidence that sexual stimulation negatively impacted the growth or immunocompetence of males. On the contrary, males exposed to female odor grew significantly faster than controls, which to our knowledge is a novel finding. The increased growth of males stimulated with female odor appears to be a sexual response because males exposed to the odor of males did not gain more body mass than water stimulated controls. This odor-induced gain in body mass may be a functional response to increase a male's mating success. Although increased growth does not appear to impact immunity, it may negatively affect longevity and therefore represent a significant cost.

The paradox of mixed mating in plants



29

Thursday August 23 *Location*: University building X

Symposium 29: The paradox of mixed mating in plants

ORGANIZERS: Elizabeth Elle, Simon Fraser University, Canada
Mark Johnston, Dalhousie University, Canada

9.45-10.15	**Emmanuelle Porcher** (invited) Promising theoretical solutions to the problem of mixed mating
10.15-10.45	**David Moeller** (invited) Evolution and biogeography of mating system variation in plants
10.45-11.05	**Pierre-Olivier Cheptou** The evolution of dispersal/outcrossing syndrome in spatially heterogeneous pollination environment: why are there so many dioecious plants on islands?
11.05-11.35	*Coffee*
11.35-11.55	**Matthew Olson** Neighborhood sex ratio and hermaphrodite selfing rate in gynodioecious populations of Silene vulgaris
11.55-12.15	**Åsa Lankinen** Delayed stigma receptivity in Collinsia heterophylla in relation to pollen competition, mating-system evolution and sexual conflicts
12.15-12.35	**Carine Collin** Influence of enemies on plant mating systems: weevils impact on selfing rates
12.35-12.55	**Xavier Vekemans** Shift in mating system along the Arabidopsis thaliana lineage: genetics, timescale and mixed mating intermediate stages
12.55-14.00	*Lunch*

29-01 Talk

PROMISING THEORETICAL SOLUTIONS TO THE PROBLEM OF MIXED MATING

Emmanuelle Porcher [1], Pierre-Olivier Cheptou [2], Christopher G. Eckert [3], Mark O. Johnston [4], John K. Kelly [5]

[1] *Muséum national d'Histoire naturelle, Laboratoire 'Conservation des Espèces, Restauration et Suivi des Populations', 61 rue buffon, 75005, Paris, France*
[2] *CNRS, UMR 5175 - Centre d'Ecologie Fonctionnelle et Evolutive, 1919 Route de Mende, F-34293, Montpellier cedex 05, France*
[3] *Queen's University, Dept. of Biology, K7L 3N6, Kingston, Ontario, Canada*
[4] *Dalhousie University, Dept. of Biology, 1355 Oxford St., B3H 4J1, Halifax, Nova Scotia, Canada*
[5] *University of Kansas, Dept. Ecology and Evolutionary Biology, 1200 Sunnyside Ave., 66045-7534, Lawrence, KS, USA*

porcher@mnhn.fr

The evolution of plant mating systems has long attracted the attention of both population geneticists and plant ecologists. However, theoretical approaches within both fields have generally been developed along independent paths: population geneticists focused mostly on the antagonistic effects of the automatic advantage of selfing versus inbreeding depression, with a variety of underlying genetic models, whereas ecologists explored factors such as pollination biology and reproductive assurance, population dynamics or resource allocation. Taken separately, these approaches usually fail to explain the amazing diversity of mating systems observed in natural plant populations, and specifically the widespread maintenance of intermediate selfing rates (the so-called “paradox of mixed mating systems”). In addition, the outcomes of genetic models often depend strongly on the overly simplified assumptions with respect to ecology, and vice versa. We thus emphasize that the population genetic and ecological traditions should be synthesized. We first present promising results obtained by incorporating both approaches, and then propose future avenues for the theoretical study of plant mating system evolution. Finally, we outline how model predictions can be addressed with experimental data.

29-02 Talk

EVOLUTION AND BIOGEOGRAPHY OF MATING SYSTEM VARIATION IN PLANTS

David A. Moeller [1], Risa D. Sargent [2], Christopher G. Eckert [3], Elizabeth Elle [4], Monica A. Geber [5], Carol Goodwillie [6], Susan Kalisz [7], Richard H. Ree [8], Alice A. Winn [9]

[1] *University of Minnesota, Department of Plant Biology, Saint Paul, MN 55108, USA*
[2] *University of California, Berkeley, Department of Integrative Biology, Berkeley, CA 94720, USA*
[3] *Queen’s University, Department of Biology, Kingston, ON KZL 3N6, Canada*
[4] *Simon Fraser University, Department of Biological Sciences, Burnaby, BC V5A 1S6, Canada*
[5] *Cornell University, Department of Ecology and Evolutionary Biology, Ithaca, NY 14853, USA*
[6] *East Carolina University, Department of Biology, Greenville, North Carolina 27858, USA*
[7] *University of Pittsburgh, Department of Biological Sciences, Pittsburgh, PA 15260, USA*
[8] *The Field Museum of Natural History, Department of Botany, Chicago, IL 60605, USA*
[9] *Florida State University, Department of Biological Science, Tallahassee, FL 32306, USA*

moell021@umn.edu

Plant mating systems are remarkably diverse and are considered to be among the most evolutionarily labile features of plants. Decades of empirical investigations have documented mating system variation among plant populations, and have explored the causes and consequences of mating system evolution. Despite this rich history of study, there remains considerable debate over the distribution of mating system variation and the role of ecological and genetic factors in directing mating system evolution. We have exploited a comprehensive database on estimates of outcrossing rates along with a phylogeny of seed plants to identify the ecological, genetic, and morphological factors that are most closely associated with mating system variation. In addition, we describe global biogeographic patterns of mating system variation and the factors that contribute to spatial patterns. Based on these results, we evaluate the possible mechanisms that may constrain plants from achieving complete outcrossing or selfing. and thus lead to mixed mating.

29-03 Talk

THE EVOLUTION OF DISPERSAL/OUTCROSSING SYNDROME IN SPATIALLY HETEROGENEOUS POLLINATION ENVIRONMENT: (WHY ARE THERE SO MANY DIOECIOUS PLANTS ON ISLANDS?)

Cheptou Pierre-Olivier [1], François Massol [1]

[1] *Centre d'Ecologie Fonctionnelle et Evolutive, CNRS, 1919, route de Mende, 34293, Montpellier, France*

pierre-olivier.cheptou@cefe.cnrs.fr

Uncertain pollination environment is often put forward as an important selection pressure favouring self-fertilisation (Darwin, 1876). Empirical results have also reported that pollen limitation is common in plants and may vary both spatially and temporally (Burd, 1994), potentially resulting in local extinction of populations (Groom, 1998). In this context, Baker (1955) made the predictions that colonizers (or dispersers) should self-fertilise to cope with pollination uncertainty.

We construct an ESS model for the joint evolution of seed dispersal and self-fertilisation in an infinite patch environment where pollination varies both spatially and temporally. Our aim was ultimately to analyse the possibility for the evolution of dispersal/outcrossing syndrome.

First, our results showed that mixed selfing rate can easily evolve in spatially heterogeneous pollination environment. Second, we found that dispersers (respectively non-dispersers) are always associated with outcrossers (respectively selfers) when both traits are free to evolve. Our predictions are in contradiction with Baker's predictions. This may however highlight the "paradoxical" high frequency of dioecious plants found on islands.

29-04 Talk

NEIGHBORHOOD SEX RATIO AND HERMAPHRODITE SELFING RATE IN GYNODIOECIOUS POPULATIONS OF SILENE VULGARIS

Matthew S. Olson [1], Keiko Miyake [1]

[1] *University of Alaska Fairbanks, Institute of Arctic Biology, 902 N. Koyukuk Rd., 99775, Fairbanks, AK, USA*

matt.olson@uaf.edu

In gynodioecious species, local sex ratio can have profound influences on relative fitnesses of hermaphrodites and females. Here we show that hermaphrodite selfing rates are increased when local frequencies of hermaphrodites are low. In two mapped roadside populations in western Virginia, we collected seed from 2 classes of hermaphrodites: 1) those with low frequencies of other hermaphrodites within 3 m and 2) those with high frequencies of other hermaphrodites within 3 m. Seeds were germinated, DNA extracted and genotypes at 5 microsatellite loci were determined for ~9 progeny per plant. Selfing rate was estimated using MLTR and the two neighborhood sex ratio classes were compared using the GROUP command. Hermaphrodites with few other hermaphrodites within 3 m had significantly higher selfing rates than hermaphrodites surrounded by high frequencies of hermaphrodites within 3m (Population 1 $P < 0.05$; Population 2 $P < 0.07$; bootstrap percentile test). We interpret these findings with respect to the influence of inbreeding depression and population subdivision on the spread of females in gynodioecious species. Our studies indicate that ecological factors such as local densities of hermaphrodites can have a strong influence on selfing rate.

29-05 Talk

DELAYED STIGMA RECEPTIVITY IN COLLINSIA HETEROPHYLLA IN RELATION TO POLLEN COMPETITION, MATING-SYSTEM EVOLUTION AND SEXUAL CONFLICTS

Åsa Lankinen [1], Samuel Kiboi [2]

[1] *Lund University, Plant ecology and systematics, Ecology building, 22362, Lund, Sweden*
[2] *University of Nairobi, Botany, Box 30197 - GPO 00100, Nairobi, Kenya*

asa.lankinen@ekol.lu.se

To understand how mating systems evolve it is important to study their relationship with specific floral traits. Species of *Collinsia* (Plantaginaceae) show extensive variation in mating system; this variation is associated with variation in floral morphology and development, and with the timing of self-pollination. Large-flowered, more out-crossing species also tend to delay stigma receptivity. This may enhance pollen competition either between different donors or between self pollen. Competition between self pollen may be of particular importance in mixed-mating species because it can lead to reduced inbreeding depression. On the other hand, possessing this trait may result in selection of pollen that manipulate onset of stigma receptivity to secure paternity at the expense of the female reproductive function. We evaluated the potential occurrence of this kind of sexual conflict by testing "female" control of timing of stigma receptivity in large-flowered *Collinsia heterophylla*. By performing one-donor crosses, we found that both recipients and pollen donors influenced when stigmas became receptive. Self pollen was further able to fertilise seeds earlier during floral development compared to outcross pollen. These results suggest that "female" control on timing of stigma receptivity is not complete in this species. In addition, crosses that succeeded early during floral development resulted in fewer seeds than later crosses, possibly indicating a cost of less control over onset of receptivity. The ability of pollen donors to influence timing of stigma receptivity might reflect a conflict between the sexual functions in *Collinsia heterophylla*. If, however, delaying stigma receptivity can reduce inbreeding depression this might outweigh the disadvantage of being fertilised by manipulative outcross pollen.

29-06 Talk

INFLUENCE OF ENEMIES ON PLANT MATING SYSTEMS: WEEVILS IMPACT ON SELFING RATES

Laurent Penet [1], Carine L. Collin [1], Tia-Lynn Ashman [1]

[1] *University of Pittsburgh, Biological Sciences, Fifth Ave and Ruskin, 15260, Pittsburgh, PA, United States*

clc155@pitt.edu

Mating system is thought to structure genetic diversity at a local scale. Thus, understanding ecological factors affecting mating system variation is cardinal to understanding the evolution of both plant and animal populations. While theoretical studies have primarily focused on genetic factors (e.g. inbreeding depression) to explain variation in mating system, sometimes empirical findings do not match perfectly those theoretical predictions. Recently, the focus has turned to understand how the ecological context can influence mating system variation with a special focus on plant-pollinator interactions. However, natural enemies represent another important aspect of ecological context of many plant species and have received little attention despite their potentially dramatic influence on mating system.

We investigated the impact of a specialist florivore (*Anthonomus signatus*, the strawberry clipping weevil) on the wild Virginian strawberry *Fragaria virginiana*. To investigate the potential consequences of weevil damage on the strawberry mating system, we assessed the direct role of these florivores on selfing rates. Clipping weevils were artificially introduced to experimental strawberry populations and selfing rates were estimated for attacked plants. We found that they can affect the plant-pollinator interaction by altering plant attractiveness, but that the consequences for mating system depended on the mode self pollination: reduced pollinator visitation in *Fragaria* lead to increased selfing via autogamy. We also quantified the intensity of weevil attack under natural conditions and we found that it did not influence individual plants selfing rates, but the local plant and genetic structure did.

29-07 Talk

SHIFT IN MATING SYSTEM ALONG THE ARABIDOPSIS THALIANA LINEAGE: GENETICS, TIMESCALE AND MIXED MATING INTERMEDIATE STAGES

Xavier Vekemans [1], Maria-Valeria Ruggiero [1]

[1] *Université de Lille 1, UMR CNRS 8016 GEPV, Bat. SN2, 59655, Villeneuve d'Ascq, France*

xavier.vekemans@univ-lille1.fr

Classic models for the evolution of plant mating systems have often considered genetic details for the control of selfing rate as a black box. Recent studies, however, have shown that genetic determination of mating systems may have a large influence on (1) the likelihood of a shift in mating system, (2) the nature of the new evolutionary stable strategy, and (3) the timescale of the shift. Although explicit models still need to be explored more extensively, advance in the field of mating system evolution in plants now critically depends on better knowledge of the genetics of mating systems in natural populations, and on the time scale of inferred evolutionary shifts. Plant families with known self-incompatibility systems represent excellent empirical models to study shifts in mating systems as investigation on the incompatibility locus will necessarily throw some light on the mechanism and timescale of the shift. We will review the results from recent studies on the genetic mechanisms of overall breakdown of self-incompatibility in *Arabidopsis thaliana*, and discuss these in the light of the recent models on mating system evolution. Then we will present new data inferring the timescale of mating system change along the *A. thaliana* lineage. These data suggest that the shift to complete self-compatibility is a very recent event in the history of the lineage, but it is not clear whether stages with a polymorphic mating system have occurred for substantial time periods. The issue of stability of such mixed mating systems will be discussed by putting together current theoretical and empirical knowledge.

29-01 Poster

MOLECULAR DIVERSITY AMONG ALLELIC COPIES OF FUNCTIONALLY EQUIVALENT SELF-INCOMPATIBILITY SPECIFICITIES IN THE GENUS ARABIDOPSIS : ASSESSING THE IMPORTANCE OF RECOMBINATION AND HYBRIDIZATION.

Vincent Castric [1], Rim Noureddine [1], Stéphane Grenier [1], Jesper Bechsgaard [2], Mikkel H. Schierup [2], Xavier Vekemans [1]

[1] *CNRS-Universite de Lille 1-Laboratoire GEPV, Batiment SN2-Cite Scientifique, 59655, Villeneuve d'Ascq, France*
[2] *Bioinformatics Research Center, University of Aarhus, Høegh Guldbergsgade 10, 8000, Århus, Denmark*

Vincent.Castric@univ-lille1.fr

Self-incompatibility systems in plants are genetic systems that prevent self-fertilisation in hermaphrodites. In the brassicaceae, the coadapted S-locus receptor kinase (SRK) and S-locus cystein rich protein (SCR) genes control pistil and pollen specificity, respectively, thus causing balancing selection to maintain a large number of highly divergent alleles at these genes. Allelic copies encoding a given specificity, however, are expected to coalesce more rapidly than allelic copies at unlinked neutral genes. Theory thus predicts 1) low polymorphism among allelic copies of functionally equivalent specificities and 2) rapid lineage sorting within specificities among closely related species, making these genes potentially powerful markers to detect hybridization.

We tested these predictions by investigating SRK sequence polymorphism among allelic copies within four specificities in Arabidopsis halleri and one in A. lyrata from natural populations collected across their distribution range. As predicted, sequence polymorphism was very low. We found no shared polymorphism within specificities, and thus no evidence for ongoing hybridization between the two species. However, we found strong evidence for intragenic recombination, thus excluding sequence-specific processes from potential explanations for recombination suppression in this region.

29-02 Poster

MUTUALISTS AND PLANT MATING SYSTEMS: BACK TO THE ROOTS

Carine L. Collin [1], Tia-Lynn Ashman [1]

[1] *University of Pittsburgh, Biological Sciences, Fifth Ave and Ruskin, 15260, Pittsburgh, PA, United States*

clc155@pitt.edu

The impact of mutualist and antagonist partners on plant mating system is recognized as an important factor shaping mating systems evolution. In addition to the indirect effects exerted via pollinators and often resulting in mixed mating systems, it is also important to consider the effects on components driving mating system evolution. The reduction of fitness experienced by selfed compared to outcrossed offspring, known as inbreeding depression, is likely to be influenced by interactions with mutualists and antagonists. We investigated this by quantifying the intensity of the relationship between a plant and its arbuscular mycorrhizal fungi. The underlying assumption being that selfed plants are less fit and thus poorest hosts to mutualists fungi. The wild strawberry *Fragaria virginiana* (Rosaceae) is naturally colonized in natural populations. We examined the level of mycorrhizal infection of selfed and outcrossed plants under semi-natural conditions. We found that inbred plants were significantly less colonized than outcrossed ones, as measured by the incidence and the intensity of hyphal colonization. The same trend was found for the intensity of vesicular colonization though it was only marginally significant. These findings suggest the association between plants and mycorrhizal fungi might further impact the level of inbreeding depression.

29-03 Poster

MANAGEMENT OF GENETIC DIVERSITY OF A CLONALLY PROPAGATED CROP IN A TRADITIONAL AMERINDIAN FARMING SYSTEM

Anne Duputié [1], François Massol [1], Patrice David [1], Claudie Haxaire [2], Doyle McKey [1]

[1] *CEFE-CNRS UMR5175, 1919 Route de Mende, 34293, MONTPELLIER CEDEX 5, France*
[2] *Université de Bretagne Occidentale, Atelier de Recherche Sociologique, 20 rue Duquesne CS 93837, 29238, BREST CEDEX 3, France*

anne.duputie@cefe.cnrs.fr

The Wayampi Amerindians of inner French Guiana cultivate about 80 cassava landraces (‘varieties’). Cassava (*Manihot esculenta* Crantz) is a clonally propagated crop which has retained the capacity for sexual reproduction. Previous studies have documented the mixed clonal/sexual reproductive system of cassava under Amerindian management. Seedlings are always recognized as being *assignable* to a variety; however, only some of them actually are *incorporated* into the stock of stem cuttings of the variety. Therefore, varieties are (mostly) not monoclonal. Wayampi women farmers remember for a few years which of their plants of each variety are issued from recent sexual reproduction events.

Like other Amerindians, Wayampi farmers usually plant cassava in monovarietal patches, made of a few clones. Therefore, seedlings are on average more homozygous than the varieties. Pujol *et al.* (2005) showed that the Palikur Amerindians unconsciously selected the most heterozygous plants by weeding. The Wayampi do not weed—probably because weeds are less of a problem in the longer fallow periods they practice—and they incorporate seedlings into varieties independently of their degree of heterozygosity, at least during the first few years of genotype testing. On the contrary, the seedlings that are chosen to be incorporated into a variety show higher genetic relatedness with the variety than do seedlings assigned to the variety, but not incorporated into it. Genetic variation among cassava clones is thus maintained in a way that preserves the genetic homogeneity of most varieties. Differences in farming practices between the Palikur and the Wayampi thus affect microevolutionary dynamics in their cassava populations.

29-04 Poster

CHANGE OF MATING SYSTEM IN THE WILD CABBAGE, BRASSICA CRETICA

Kristina Edh [1], Björn Widén [2], Alf Ceplitis [1]

[1] *Lund University, Department of Cell and Organism Biology, Sölvegatan 29, 223 62, Lund, Sweden*
[2] *Lund University, Plant Ecology and Systematics, Sölvegatan 29, 223 62, Lund, Sweden*

Kristina.Edh@cob.lu.se

Brassica cretica is a wild plant species in the large and important Brassicaceae family. It grows in ravines in the eastern Mediterranean region and as a result of long-term isolation, populations are extremely phenotypically and genetically differentiated. One characteristic that varies between populations is flower size, a trait that is well known to be associated with mating system. The ancestral mating system in *B. cretica* (as well as in other Brassicaceae) is outcrossing, which is maintained by a self-incompatibility (SI) mechanism. However, individuals with different levels of SI and even completely self-compatible individuals have been found in *B. cretica*.

In a study comprising 40 individuals from 4 different populations, the *S*-locus genes encoding the male and female determinants of SI were sequenced and a high level of molecular diversity as well as a large number of haplotypes was revealed. A population from Moni Kapsa on eastern Crete was found to have the highest number of self-compatible individuals in experimental crosses and this population also has very small petals compared to other populations. Individuals from Moni Kapsa were used in greenhouse crosses and we found that self-compatibility and the *S*-locus did not segregate independently. We also found that the ability to set seeds after selfing is associated with one or more haplotypes of the more recessive dominance class (class II). We suggest that the *B. cretica* mating system is currently changing from outcrossing to selfing.

29-05 Poster

BAYESIAN ESTIMATE OF THE FULL INTER-INDIVIDUAL VARIANCE OF MALE FECUNDITY TOGETHER WITH THE DISPERSAL KERNEL: APPLICATION TO SORBUS TORMINALIS (L.) CRANTZ.

Etienne K. Klein [1, 2], Nicolas Desassis [1], Sylvie Oddou-Muratorio [2]

[1] *INRA Avignon, UR 546 Biostatistique et Processus Spatiaux, Domaine Saint Paul, Site Agroparc, 84914, Avignon, France*
[2] *INRA Avignon, UR 629 Recherches Forestières Mediterranéennes, Domaine Saint Paul, Site Agroparc, 84914, Avignon, France*

etienne.klein@avignon.inra.fr

Inter-individual variance of male reproductive success (MRS) contributes to genetic drift, that interacts in turn with selection and migration to determine the short-term response of populations to rapid changes in their environment. Individual MRS can be estimated through paternity analysis but a further step is to decompose the MRS into a fecundity and a spatial components. Existing methods that achieve this decomposition either rely on the strong assumption of a random distribution of pollen donors (TwoGener) or estimate only the part of the variance of male fecundity explained by few covariates. We developed a new method to estimate jointly (i) the full variance of male fecundity, (ii) the pollen dispersal kernel and (iii) the selfing and immigration rates, from the genotypes of sampled seeds and exhaustive positions and genotypes of putative fathers. We modelled the individual fecundities as a random effect assumed log-normal. We used a Bayesian approach well suited to the hierarchical model proposed.
When applied to Sorbus torminalis, the estimated variance of male fecundity led to an effective density of trees 13 times lower than the observed density (dobs/dem ~13). This value is intermediate between dobs/dem ~2 estimated in the classical mating model with three major covariates affecting fecundity and dobs/dem ~30 estimated with TwoGener. Estimates for the dispersal kernel, selfing rate and immigration rate were close to previous results (mean dispersal distance~700m, fat-tailed dispersal kernel with b=0.3 for an exponential power function, immigration rate ~ 43% and selfing rate ~0.5%). We further investigated whether individual fecundities are (i) spatially correlated, (ii) annually varying and (iii) genetically heritable.

29-06 Poster

INFLUENCE OF GENETIC LOAD ON DYNAMICS OF DOMINANCE AND FREQUENCY OF SELF-INCOMPATIBILITY ALLELES: MODELS AND APPLICATION TO ARABIDOPSIS HALLERI

Violaine C. Llaurens [1], Sylvain Billiard [1], Lucy Gonthier [1], Jean-Baptiste Leducq [1], Vincent Castric [1], Xavier Vekemans [1]

[1] *Laboratoire GEPV (UMR CNRS 8016), Biology, Bat SN2 Universite des sciences et techniques de Lille 1, 59655, Villeneuve d'Ascq cedex, France*

violaine.llaurens@ed.univ-lille1.fr

Self-incompatibility is a widespread phenomenon in flowering plants: it avoids selfing and reproduction with relatives. This system is controlled by a single highly polymorphic locus. This S-locus encodes for specificities expressed in pollen and pistil: reproduction is only possible between pollen and pistils carrying different specificities. The high polymorphism observed at the S-locus seems to be maintained by negative frequency-dependent selection. In *Arabidopsis halleri*, the specificities of pistil and pollen are both determined by the diploid parental genotype and depend on the dominance interactions between parental S-alleles at S-locus. Theoretical studies have shown that the dynamics and frequency distribution of S-alleles depend on the patterns of dominance relationships among them. Moreover, as the S-locus and its flanking regions have a low recombination rate and high heterozygosity, an accumulation of deleterious mutations linked to S-alleles was hypothesized, which also influences evolution of S-allele frequencies. This linked genetic load is predicted stronger when the associated S-allele is dominant. We investigate evolution of dominance among S-alleles under a deterministic model which simulates changes in S-allele frequencies under frequency-dependent selection. We show that evolution of dominance is positively selected, and modified by the genetic load linked to the S-locus. We compare these theoretical results to empirical data in a small isolated population in which we determined the number and frequencies of S-alleles, dominance relationships among them, and the genetic load linked to each S-alleles.

29-07 Poster

EVOLUTION OF INBREEDING DEPRESSION IN SPECIES COMBINING SELF-INCOMPATIBILITY AND ASEXUAL REPRODUCTION

Miguel Navascués [1], Solenn Stoeckel [2], Stéphanie Mariette [3]

[1] *ENS, 75005, Paris, FRANCE*
[2] *UMR 8079, UPS/CNRS/INAPG/ENGREF, 91405, Orsay, FRANCE*
[3] *INRA, 33883, Villenave d'Ornon, FRANCE*

smariett@bordeaux.inra.fr

The origin and maintaining of self-incompatibility systems in angiosperms are still debated questions. Based on the study of interactions between viability loci, causing inbreeding depression, and the S-locus, Charlesworth and Charlesworth (1979) demonstrated that self-compatibility can secondarily evolve through the breakdown of a SI system if inbreeding depression is small enough. The level of inbreeding depression in species that show a self-incompatibility system is a key parameter for the maintenance of the system. Several studies were developed to predict when the system can breakdown. In species combining both self-incompatibility and asexual reproduction, we hypothesize that the maintenance of the SI system may be due to the maintenance of inbreeding depression not only on locus directly linked to the S locus, but at the genome level due to asexual reproduction.

We developed a model to simulate the evolution of inbreeding depression in a diploid species that reproduce both asexually and sexually with a self-incompatibility system. Four loci were studied: the S-locus that determines self-incompatibility, a viability locus and two neutral loci. We simulated different scenario, varying the population size, the selection intensity and the asexual reproduction rate. Results of this model will be presented.

29-08 Poster

THE MATING SYSTEM OF VRIESEA GIGANTEA GAUD. (BROMELIACEAE): A MOLECULAR-MARKER BASED INVESTIGATION OF PROGENY ARRAYS FROM NATURAL POPULATIONS

Gecele Matos Paggi [1], Clarisse Palma da Silva [1], Thelma Barbará [2], Maria Helena Bodanese Zanettini [1],
Christian Lexer [2], Fernanda Bered [1]

[1] *Universidade Federal do Rio Grande do Sul, Laboratório de Genética Vegetal, IB, Porto Alegre, RS, Brazil*
[2] *Royal Botanic Gardens, Jodrell Laboratory, Kew, Richmond, Surrey, TW9 3DS, UK*

gecelepaggi@yahoo.com.br

The reproductive system is directly related to the genetic structure and diversity of natural plant populations. Little is known about the ecological impact and evolutionary outcome of natural variation in breeding systems in non-model species. *Vriesea gigantea* is an epiphytic bromeliad which occurs in the Atlantic Rainforest, Brazil. Information about its reproductive system and outcrossing rates is needed to develop efficient conservation strategies. In addition to our field studies of pollination and reproductive biology, the 'progeny-pair' analysis of highly informative microsatellite markers provides accurate and detailed information about the reproductive system of *V. gigantea*. These estimates can be generated by examining allelic variation over many loci in progeny arrays from plants allowed to pollinate naturally, using maximum-likelihood approaches to exclude progeny resulting from self-fertilization. Our objective is to fill an important gap in our knowledge of the reproductive biology of this ecologically and horticulturally important bromeliad. We will present estimates of outcrossing rates using microsatellite loci and progeny arrays from natural populations. Results of this research will be discussed in the light of recent findings on the role of pollinator and resource limitation in constraining fertility and population viability in this species (Paggi et al. 2007, American Journal of Botany 94: 683-689). The conservation implications of the observed patterns of inbreeding coefficients and outcrossing rates will be discussed.

29-09 Poster

PREDOMINANCE OF OUTCROSSING IN LYMNAEA STAGNALIS DESPITE LOW APPARENT FITNESS COSTS OF SELF-FERTILIZATION

Mikael Puurtinen [1], Emily Knott [1], Susanna Suonpää [1], Kari Nissinen [1], Veijo Kaitala [2]

[1] *University of Jyväskylä, Finland*
[2] *University of Helsinki, Finland*

hemipu@bytl.jyu.fi

We have quantified the natural mating system in eight populations of the simultaneously hermaphroditic aquatic snail *Lymnaea stagnalis*, and studied the ecological and genetic forces that may be directing mating system evolution in this species. We investigated whether the natural mating system can be explained by the availability of mates, by the differential survival of self- and cross-fertilized snails in nature, and by the effects of mating system on parental fecundity and early survival. The natural mating system of *L. stagnalis* was found to be predominantly cross-fertilizing. Density of snails in the populations had no relationship with the mating system, suggesting that outcrossing rates are not limited by mate availability at the population densities observed. Contrary to expectations for outcrossing species, we detected no evidence for inbreeding depression in survival in nature with inferential population genetic methods. Further, experimental manipulations of mating system in the laboratory revealed that self-fertilization had no effect on parental fecundity, and only minor effects on offspring survival. Predominance of cross-fertilization despite low apparent fitness costs of self-fertilization is at odds with the paradigm that high self-fertilization depression is necessary for maintenance of cross-fertilization in self-compatible hermaphrodites.

29-10 Poster

GENETIC STRUCTURE OF PLANTS THAT COMBINED SEXUAL REPRODUCTION UNDER GAMETOPHYTIC SELF-INCOMPATIBILITY SYSTEMS AND ASEXUAL PROPAGATION: DATA FROM PRUNUS AVIUM L.

Solenn Stoeckel [1], Jérôme Grange [2], Stéphanie Mariette [3]

[1] *Cemagref/Paris-sud University/UPMC, Laboratoire Ecologie, Systématique et Evolution, Bat. 360, 1er étage, porte 302, 91405, Orsay, France*
[2] *Cemagref, Unité de Recherche 'Ecosystèmes Forestiers', Domaine des Barres, 45290, Nogent-sur-Vernisson, France*
[3] *INRA/Cemagref, Unité de Recherche sur les Espèces Fruitières et la Vigne, Domaine de la Grande Ferrade, 71 avenue Edouard Bourlaux, 83, Villenave d'Ornon, France*

solenn.stoeckel@u-psud.fr

Mating systems hold key parameters to understand the evolutionary processes shaping both the genetic diversity and differentiation. Most plants can propagate through both vegetative and sexual reproduction under gametophytic self-incompatibility systems (GSI). Furthermore, a recent phylogenetic analysis show that self-incompatibility is strongly associated with clonal reproduction (Vallejo-Marin & O'Brien 2006). Even so, the population genetic of such mixed mating systems remain unclear. Because plants are sessile organisms, asexual propagation tends to aggregate genotype and genetic diversity while sexual reproduction under GSI favours genetic mobility, at least in the vicinity of the GSI-involved loci (Glémin *et al.* 2001; Balloux 2004).

The aim of our study was to improve the understanding of the impact of the two reproductive strategies on both genetic diversity and differentiation through time. We used filed and genetic data (8 microsatellites and genetic markers probing the self-incompatibility locus) to study 3 populations of wild cherry trees, a scattered, entomophilous and hermaphroditic species that combined sexual reproduction under GSI and asexual propagation through suckering roots. We also used spatialized individual-based simulations to explore the conjoint effects of such mating systems. The results will be discussed and compared to predictions formulated from previous theoretical works (Bengtsson 2003; Balloux *et al.* 2003; De Meeus & Balloux 2005; Prugnolle *et al.* 2005).

29-11 Poster

PATTERNS OF SELF-INCOMPATIBILITY IN ROSACEAE

Cristina P. Vieira [1], Jorge Vieira [2]

[1] *University of Porto/IBMC, Molecular Evolution, Rua do Campo Alegre 183, 4150-180, Porto, Portugal*
[2] *University of Porto/IBMC, Molecular Evolution, Rua do Campo Alegre 823, 4150-180, Porto, Portugal*

cgvieira@ibmc.up.pt

Self-incompatibility (SI) is a mechanism present in flowering plants that prevents self-fertilisation, by enabling the pistil to reject pollen from genetically related individuals. In gametophytic SI (GSI) pollen specificity is determined by the *S*-locus genotype of the haploid gametophyte. Under the theoretical framework of SI the number and frequency of S - alleles follows an equilibrium between selection, mutation and drift where the alleles are maintained at equal frequencies if they are selectively equivalent. The expectation of equal frequencies in populations at equilibrium holds in general for Solanaceae species but not for Rosaceae species. In agreement with the findings for other Rosaceae species (*Prunus avium* and *P. lannesiana*, *Crataegus monogyna* and *Sorbus aucuparia*) in *P. spinosa* unequal frequencies are also observed. Possible reasons for the different patterns observed in Solanaceae and Rosaceae are discussed, such as selection on linked loci, founder effects, the presence of null alleles and vegetative propagation.

When is a hierarchical model not appropriate in plant systematics

30

Friday August 24 *Location*: University building IX

Symposium 30: When is a hierarchical model not appropriate in plant systematics

ORGANIZERS: Bengt Oxelman, Uppsala Univeristy, Sweden
Katharina Huber, University of East Anglia, UK

9.45-10.15	**Peter Lockhart** (invited) Species radiation in the New Zealand alpine flora
10.15-10.45	**Vincent Moulton** (invited) Using networks to explore non-hierachical patterns of evolution in plants
10.45-11.05	**Katarina Andreasen** Potential hybridization in real data sets: complex relationships in young flowering plants
11.05-11.35	*Coffee*
11.35-11.55	**Anja Rautenberg** Recombination between distinct lineages in Silene?
11.55-12.15	**Božo Frajman** Hybrid origins and homoploid reticulate evolution within Heliosperma (Sileneae, Caryophyllaceae) – a multigene phylogenetic approach
12.15-12.35	**Guido Grimm** ITS evolution in Platanus: homoeologues, pseudogenes, and ancient hybridisation
12.35-14.00	*Lunch*
14.00-14.20	**Christian Lexer** Evolutionary outcomes of hybridization in Populus
14.20-14.40	**Simon Joly** On the phylogeny of organisms using allelic variation and its relevance for studying non-hierarchical evolution
14.40-15.00	**Mattias Jakobsson** The number of genetic founding lineages
15.00-15.20	**Bengt Sennblad** Extending models of genome evolution to include non-hierarchical events
	Coffee

30-01 Talk

SPECIES RADIATION IN THE NEW ZEALAND ALPINE FLORA

Peter J. Lockhart [1], Heidi Meudt [2]

[1] *Massey University, Allan Wilson Centre for Molecular Ecology and Evolution, Institute of Molecular BioSciences, New Zealand*
[2] *Museum of New Zealand, Te Papa Tongarewa, Wellington, New Zealand*

p.j.lockhart@massey.ac.nz

Late Tertiary/Quaternary plant species radiations are a feature of alpine floras. In the high-elevation regions of New Zealand, multiple genera have radiated to produce ecologically and morphologically distinct yet genetically similar species. The biological complexity of these radiations is difficult to describe in terms of hierarchical models of evolution. This is because species divergence may not be bifurcating and because evolutionary properties of sequences/limitations of phylogenetic methodology make reconstruction a difficult problem. In this talk, we outline these issues and the questions of species radiation being investigated for the New Zealand alpine flora.
http://awcmee.massey.ac.nz/NZPRN/themes.htm. We discuss and explain ideas that have motivated the development of recent and novel analytical methods now being used to study plant evolutionary histories [1].

[1] McBreen and Lockhart (2006) Reconstructing reticulate evolutionary histories of plants. Trends Plant Sci. 2006 11, 398-404

30-02 Talk

USING NETWORKS TO EXPLORE NON-HIERACHICAL PATTERNS OF EVOLUTION IN PLANTS

Vincent Moulton [1]

[1] *University of East Anglia, School of Computing Sciences, NR4 7TJ, Norwich, UK*

vincent.moulton@cmp.uea.ac.uk

Realisation of the extent of non-hierachical patterns of evolution in nature has led to the development of network based methods of phylogenetic analysis that can help visualise and reconstruct complex evolutionary histories. In this talk, we will discuss some different methodologies for constructing such networks, with illustrations from plant evolution, together with some future directions, including potential applications and limitations of network methods.

30-03 Talk

POTENTIAL HYBRIDIZATION IN REAL DATA SETS: COMPLEX RELATIONSHIPS IN YOUNG FLOWERING PLANTS

Katarina Andreasen [1]

[1] *Uppsala University, Systematic Botany, Norbyv. 18D, 75236, Uppsala, Sweden*

Katarina.Andreasen@ebc.uu.se

The reticulate nature of hybridization violates the basic assumption of bifurcation when reconstructing phylogenetic trees with the commonly used methods. Different approaches have been used to deal with this problem in phylogenetics: first to try to identify and remove hybrids before the phylogenetic analysis, second to detect hybrids by their behavior in the trees, and third to compare incongruent postions between trees constructed from independent data sets. I will give examples on the feasability of identifying hybrids both in theory and practice in phylogenetic analyses. The study groups are two young flowering plant genera (Arnica, Asteraceae and Sidalcea, Malvaceae) for which several hybridization hypotheses have been suggested. The results show that using artifical hybrids reticulation is easily detected but that the situation becomes much more complex when potential hybrids in natural populations are involved.

30-04 Talk

RECOMBINATION BETWEEN DISTINCT LINEAGES IN SILENE?

Anja Rautenberg [1], Bengt Oxelman [1, 2]

[1] *Uppsala University, Department of Systematic Botany, Norbyv. 18D, SE-752 36, Uppsala, Sweden*
[2] *Göteborg University, Department of Plant and Environmental Sciences, Box 461, SE-405 30, Göteborg, Sweden*

anja.rautenberg@ebc.uu.se

One of the challenges of evolutionary biologists is to reconstruct phylogenies, which are essential in order to understand the mechanisms of evolution. In systematic research, often only very small portions of the total genome are analyzed and assumed to reflect the species phylogeny. In principle, however, the resulting phylogenies do not reflect the history of the species, but rather the history of the individual DNA regions themselves. Sometimes the phylogenies show incongruences when based on different genomes, different genes, different copies of a gene, or different parts of a gene. These conflicts can either reflect complex phylogenetic patterns, or simply highlight errors and problems in lab procedures and/or phylogenetic methods. An example of a plant taxon with cases of conflicting gene phylogenies is Sileneae DC. (Caryophyllaceae). Silene section Elisanthe contains dioecious taxa with a X/Y chromosome system similar to that in humans. In order to understand the evolution of dioecy in Silene section Elisanthe, we compare the dioeciuos taxa with their closest relatives, using several molecular markers. We also test the utility of the potentially useful low-copy nuclear gene SlX1/SlY1, and its homologues in hermaphroditic taxa. We discovered that Elisanthe change places in the phylogenetic trees based on different parts of the SlX1/SlY1 alignment. We show that this may indicate that recombination between phylogenetically distant SlX1/SlY1 lineages has taken place.

30-05 Talk

HYBRID ORIGINS AND HOMOPLOID RETICULATE EVOLUTION WITHIN HELIOSPERMA (SILENEAE, CARYOPHYLLACEAE) – A MULTIGENE PHYLOGENETIC APPROACH

Božo Frajman [1, 2], Frida Eggens [2], Bengt Oxelman [2]

[1] *University of Ljubljana, Biotechnical Faculty, Biology Department, Ve?na pot 111, 1000, Ljubljana, Slovenia*
[2] *Uppsala University, Evolutionary Biology Centre, Systematic Botany, Norbyvägen 18d, 75236, Uppsala, Sweden*

bozo.frajman@bf.uni-lj.si

We have used four potentially unlinked nuclear DNA regions from the gene family encoding the second largest subunit of the RNA polymerases (RNAP), and the chloroplast genome psbE-petG spacer and rps16 intron in the tribe Sileneae (Caryophyllaceae), to develop a framework to evaluate different phylogenetic explanations for conflicting gene trees. The relative dates of different divergence times are used to discriminate among inter- and intralineage processes causing topological conflicts between gene trees. The incongruences seen between the chloroplast DNA and nuclear regions regarding the relationships among the three major lineages of Heliosperma are best explained by homoploid hybridization. The pattern regarding the origin of Heliosperma itself is more complicated and is likely to include several reticulate events. Different RNAP regions suggest that at least two different lineages have been involved in the origin of Heliosperma. One lineage is most closely related to Viscaria/Atocion and the other is closer to Eudianthe and/or Petrocoptis.

30-06 Talk

ITS EVOLUTION IN PLATANUS: HOMOEOLOGUES, PSEUDOGENES, AND ANCIENT HYBRIDISATION

Guido W. Grimm [1], Thomas Denk [2]

[1] *University of Tübingen, Institute of Geosciences, Biogeology, Sigwartstrasse 10, 72076, Tübingen, Germany*
[2] *Natural History Museum, Palaeobotany, Box 50007, 10405, Stockholm, Sweden*

guido.grimm@uni-tuebingen.de

Platanaceae is an old family of angiosperms extending back to the Early Cretaceous but consisting of a single extant genus *Platanus*. Species of *Platanus* have long been known to hybridize, and the ‘London Plane’ *Platanus* x *hispanica* is a well-known example for a hybrid species that formed in historical times. Morphological studies suggested past interspecific or interlineage hybridisation (reticulation) as possible important factors in the evolution of the genus. The internal transcribed spacers (ITS) of the 35S nuclear ribosomal DNA cistron are a biparentally inherited, multi-copy marker with a high potential for resolving intrageneric relationships especially when ancient hybridisation (reticulation) is involved. In addition to phylogenetic trees, splits graphs and motif analysis can be used to extract phylogenetic information from 223 cloned ITS sequences. Non-pseudogenous and pseudogenous sequence motives are assessed to explain how different evolutionary modes contribute to possibly conflicting character state patterns in the ITS. Putative non-functional ITS copies (‘pseudogenes’) form independent groups in phylograms and splits graphs; distinct pseudogenous lineages reflect ancient (Palaeogene, Cretaceous) hybridisation events conserved in the ITS. Specifically, pseudogenous clones of an ‘Atlantic’ North American clade appear closest related to non-pseudogenous clones of the western (‘Pacific’) North American *P. racemosa* species aggregate. Recent lateral gene flow is evidenced as an important factor in the evolution of the Central Mexican *P. rzedowskii* including additional nuclear sequence data (2nd LEAFY intron, 5S rDNA intergenic spacer). We promote the use of broad (cloned) ITS data sets covering intra- and interindividual variability to analyse primary mechanisms of evolution: the 'feared' incompatible signals in cloned ITS sequences contain information about complex patterns and reticulate evolutionary pathways, which can be visualized with splits graphs but not with bifurcating trees.

30-07 Talk

EVOLUTIONARY OUTCOMES OF HYBRIDIZATION IN POPULUS

Christian Lexer [1], Jeffrey A. Joseph [1], Marcela Van Loo [1], Irina Hase [2], Michael F. Fay [1], Berthold Heinze [2]

[1] *Royal Botanic Gardens Kew, Jodrell Laboratory, TW9 3DS, Richmond, Surrey, United Kingdom*
[2] *Federal Research Centre for Forests, Department of Genetics, Hauptstrasse 7, A-1140, Vienna, Austria*

c.lexer@kew.org

Hybridization and introgression between divergent species are widespread phenomenona in plants. From the molecular systematist's angle, hybridization will result in conflicting genetic signatures when multiple genetic loci or genomic compartments are used for phylogenetic inference. Such indications of past hybridization and introgression indicate that a network may provide a more suitable representation of evolutionary history than a simple phylogenetic tree. This may be the case for the genus *Populus* (poplars, aspens, cottonwoods; Salicaceae). *Populus* has recently received increased attention not only because it is the first tree genus for which a complete genomic DNA sequence is available, but also because hybridization and introgression have apparently played an important role in its evolutionary history. The latter observation is of interest as hybridizing populations of *Populus* species are increasingly utilized for the development of novel concepts in population genomics, community genetics, and the genetics of speciation and species differences. We will review published phylogenetic studies suggesting that networks are sometimes more appropriate than trees to describe evolution of this genus. We will also discuss our own results on nuclear admixture and plastid DNA networks in hybridizing European *Populus* species. We will highlight the importance to distinguish between different evolutionary outcomes of past hybridization, such as hybrid speciation and the introgression of specific DNA segments or adaptive traits.

30-08 Talk

ON THE PHYLOGENY OF ORGANISMS USING ALLELIC VARIATION AND ITS RELEVANCE FOR STUDYING NON-HIERARCHICAL EVOLUTION

Simon Joly [1], David Bryant [2], Peter J. Lockhart [1]

[1] *Massey University, Allan Wilson Centre, Private Bag 11222, 4442, Palmerston North, New Zealand*
[2] *Auckland University, Department of Mathematics, Private Bag 92019, 1142, Auckland, New Zealand*

s.joly@massey.ac.nz

Alleles evolve in a tree-like fashion and their evolution can be readily reconstructed using bifurcating phylogenetic methods. Yet it is often more useful to reconstruct the phylogeny of organisms or of species and these do not always evolve following a hierarchical pattern. In this presentation, we discuss methods for reconstructing the evolutionary history of organisms by incorporating allelic variation. Using examples from *Rosa* species in North America, we then show how this approach insights on speciation, hybridization and polyploid evolution.

30-09 Talk

THE NUMBER OF GENETIC FOUNDING LINEAGES

Mattias Jakobsson [1], Noah A. Rosenberg [1]

[1] *University of Michigan, Dept. of Human Genetics, 2017 Palmer Commons, 100 Washtenaw Ave, 4809, Ann Arbor, MI, USA*

mjakob@umich.edu

In plants, hybridization and polyploidization events occur frequently, and from these events new species can instantaneously arise. These speciation events can occur in unique events, or in multiple similar events contributing to the same incipient species. The number of events that led to the founding of a species can shape the composition of genetic variation in the new species. This number of founding events can be defined as the number of ancestral individuals that contributed (at a specific locus) to a present-day derived species, and can be formulated in terms of interspecific coalescence events. We consider a neutral coalescent model of two species where a derived species is founded as an offshoot of an ancestral species. For a given locus we compute the probability distribution of the number of genetic founding lineages that have given rise to the derived species. For 99.99% of the loci in the derived species to each have one founding lineage, the two species must be separated for >=9.9N generations. However, only ~0.87N generations must pass since divergence for 99.99% of the loci to have <6 founding lineages. Our results are useful as a prior expectation on the number of founding lineages in scenarios that involve the evolution of one species from the splitting of an ancestral group, such as the formation of polyploid species, and the domestication of crops from wild ancestors. We show an application of the model of founding lineages in estimating the number of founding lineages of *Arabidopsis suecica*, an allopolyploid species formed from *A. thaliana* and *A. arenosa*.

30-10 Talk

EXTENDING MODELS OF GENOME EVOLUTION TO INCLUDE NON-HIERARCHICAL EVENTS

Bengt Sennblad [1]

[1] *Stockholm Bioinformatics Center, AlbaNova Research Center, SE-106 91, Stockholm, Sweden*

bengt.sennblad@sbc.su.se

We have developed the 'gene evolution model', the first probabilistic model for gene duplications and loss. I will briefly describe this model and how it can be integrated with standard substitution models to allow simultaneous analysis of the two processes. I will then discuss ongoing work on how to extend this model to allow non-hierarchical events such as horizontal gene transfer and allopolyploidy, both in a parsimony and a probabilistic setting.

30-01 Poster

THE CONTRIBUTION OF THE SILENE AJANENSIS (SECT. PHYSOLYCHNIS, CARYOPHYLLACEAE) GROUP TO THE FORMATION OF ARCTIC AND SIBERIAN POLYPLOIDS

Anna Petri [1], Bengt Oxelman [1]

[1] *Göteborg University, Department of Plant and Environmental Sciences, Faculty of Science, Carl Skottbergsgatan 22B, SE - 413 19, Göteborg, Sweden*

anna.petri@dpes.gu.se

The diploid Silene ajanensis group, which comprises about four taxa mainly distributed in North/Northeast Asia, has been involved in the formation of both tetraploid and hexaploid Arctic Silene. We have investigated the relation of the S. ajanensis group to three polyploid derivate taxa, as well as two taxa (S. sachalinensis and S. tolmatchevii) of unknown ploidy level, occurring in the Arctic and in Northeast Russia, using multiple gene phylogenies. Sequence data from chloroplast DNA (the rps16 intron and the psbE/petL spacer), nuclear ribosomal DNA (the internal transcribed spacers, ITS 1 and 2, and the intervening 5.8S gene) and a region from the low copy nuclear RNA polymerase (RNAP) family (RPA2, RPB2, RPD2a, RPD2b) were used. Several occurrences of within-plant polymorphisms in the RNAP genes were found and many of these can be explained by allopolyploidy, but there are two indications of independent gene duplications. This emphasizes the need to study multiple independent gene phylogenies to discriminate between whole-genome and single gene duplications. The RPD2b data suggest a close relationship between two of the taxa in the S. ajanensis group, and that this lineage has been involved in the formation of two hexaploids. Hybrid origins of S. sachalinensis and S. tolmatchevii are strongly supported. They both appear to be allotetraploids, with the S. ajanensis stem group as probable paternal lineage. S. sachalinensis is likely to stem from the diploid S. uralensis lineage on the maternal side, whereas the S. tolmatchevii maternal lineage is to be sought in the stem group of a more inclusive group, including S. uralensis. Horizontal gene transfer events in RPA2 and RPB2 are discussed.

30-02 Poster

PHYLOGENETICS, BIOGEOGRAPHY, AND CHROMOSOMAL EVOLUTION IN RUTA (RUTACEAE)

Gabriele Salvo [1]

[1] *University of Zurich, Institute of Systematic Botany, Zollikerstrasse 107, 8008, Zurich, Switzerland*

salvo@systbot.unizh.ch

The Mediterranean basin, with its complex but well-known history of microplate movements and climatic oscillations, provides the geological backdrop for the diversification of *Ruta*. In its current circumscription *Ruta* includes 8 species of perennial shrubs: four species have a peri-Mediterranean distribution (*R.chalepensis*, *R.graveolens*, *R.angustifolia*, and *R.montana*), and four species are island endemics (*R.corsica* is endemic to the Corso-Sardinian microplate; and *R.pinnata*, *R.oreojasme*, and *R.microcarpa* are endemic to the Canary Islands). Phylogenetic analyses of three chloroplast DNA regions (*mat*K, *rpl*16, and *trn*LF) support the monophyly of *Ruta*. Within *R.corsica*, the populations from Corsica and Sardinia, respectively, form two well-supported clades. This result confirms recent morphological and karyological work that identified the populations of the two islands as two species, and suggests that the Strait of Bonifacio, separating the two islands, acted as a barrier to gene flow. The inferred monophyly of the species endemic to the Canary Islands indicates a single origin of the lineage, followed by diversification within the archipelago, and the relative temporal order of splitting is congruent with the order of island formation in the Canarian archipelago. The species of *Ruta* have a different haploid number, ranging from 9 to 36, suggesting that different cytoevolutionary processes, such as polyploidy and euploid increase/decrease, might have played an important role in the evolution of this genus.

30-03 Poster

THE ROLE OF ALLOPOLYPLOIDY IN THE EVOLUTION OF THE GENUS POTENTILLA (ROSACEAE)

Mats Töpel [1]

[1] *Göteborg University, Department of Plant and Environmental Sciences, Box 461, 405 30, Göteborg, Sweden*

mats.topel@dpes.gu.se

Earlier work on the monophyly of the plant genus Potentilla (Rosaceae) has revealed that allopolyploidisation may have played a role in the formation of the group. After sequencing two nuclear regions (ITS and ETS) and two chloroplast regions (trnL-F and trnS-G) of more than 60 Potentilla species, support for this idea are now even stronger. Incongruence between the nuclear and the plastid trees is substantial and a hierarchical model for the evolution of this genus seems almost impossible to infer.

The position of the two North American genera, Ivesia and Horkelia, within Potentilla s.s. finds support in the analysis, and they form one of the incongruent groups between phylogenies indicating that hybridisation may be involved in their formation. Further work will focus on the phylogenetic history of this clade. This project is a work in progress and I will present the current state of my PH.D. project named "The role of allopolyploidy In the evolution of the genus Potentilla (Rosaceae)".

Authors