ESEB IX

European Society for Evolutionary Biology

Abstracts

9th Congress, Leeds, August 18-24, 2003

European Society for Evolutionary Biology, 9th Congress, Leeds 18-24 August 2003

Plenary sessions

EVOLUTION AND EVERYDAY LIFE: EXAMPLES OF RELEVANCE AND NEGLECT

Robert M May

EVOLUTIONARY GENOMICS: PLATFORM FOR A NEW MODERN SYNTHESIS

Daniel L. Hartl

BUTTERFLY EYESPOTS AND THE POWER OF EVO-DEVO TO EXPLORE EVOLUTIONARY CONSTRAINTS

Paul M. Brakefield

THE GENETICS OF ADAPTATION: WHAT DO WE KNOW?

H. Allen Orr

CONSERVATION GENETICS IN THE NEW MOLECULAR AGE

Robert K. Wayne

European Society for Evolutionary Biology, 9th Congress, Leeds 18-24 August 2003

Symposia

1. **Journal of Evolutionary Biology Symposium:**
   The role of evolutionary biology in understanding, preventing and treating infectious diseases.
2. Reproductive parasites in evolution
3. Genetics of species differences
4. Natural hybridization and introgression: its role in evolution and conservation
5. Evolution of non-coding DNA
6. Sexual conflict
7. Pleistocene refugia, colonization patterns and evolution
8. Are transmission modes important for the evolution of mutualistic symbiosis?
9. Genetic biodiversity in natural populations: implications for management
10. Experimental microbial evolution: the roles of sex, recombination and mutation
11. Pollinator and plant evolution – from specialists to generalists
12. Evolution of sexual communication in insects
13. Geographical parthenogenesis and polyploidy
14. Positive selection and adaptive trait genes
15. Evolutionary biology of learning
16. Key factors in adaptive radiation
17. The evolutionary biology of complex phenotypes
18. The evolution of sexual size dimorphism
19. From cell to society: conflict and cooperation at different evolutionary levels
20. The evolutionary roles of biased variation and internal selection
21. Evolution on islands – patterns of colonisation, adaptation and speciation
22. The evolutionary significance of variation in reproductive investment
23. Morphological model systems in evolution and development
24. Social plasticity
25. Genome cell size and scaling of metabolic rate: a cytogenetic approach to life history evolution
26. Theoretical & empirical aspects of the evolution of diversity: speciation, species discovery, and inventory
27. Limits to species boundaries: linking hybrid zones with adaptation to marginal conditions
28. Evolutionary consequences of mate choice
29. Evolutionary dynamics of Major Histocompatibility Complex
30. Evolution of host defence against parasites

European Society for Evolutionary Biology, 9th Congress, Leeds 18-24 August 2003

Programme Overview

	Plenary	Morning	Afternoon	Evening
Monday			Registration	Welcome Reception
Tuesday	Robert May	Symposia 1-5	Symposia 1-5	Poster Session
				'Open Access Publishing' discussion
Wednesday	Daniel Hartl	Symposia 6-10	Symposia 6-10	Presidential address
				Maynard Smith Prize lecture
Thursday	Paul Brakefield	Symposia 11-15	Excursions	Excursions
		ESEB Business Meeting	Poster change-over	
Friday	Allen Orr	Symposia 16-20	Symposia 21-25	Poster Session
				Congress Dinner
Saturday	Robert Wayne	Symposia 26-30	Symposia 26-30	
Sunday	Departure			

European Society for Evolutionary Biology, 9th Congress, Leeds 18-24 August 2003

Outline Programme

Monday 18 August

14:00	Registration Opens
18:00 – 21:00	Welcome Reception, Refectory
17:00 – 23:59	Terrace Bar open, Leeds University Union

Tuesday 19 August

08:40	Welcome	Sir Alan Wilson Vice-Chancellor, The University of Leeds
08:50	Plenary	Robert May
		Evolution and Everyday Life: Examples of relevance and Neglect
	Chair	Jacobus Boomsma
09:50	Symposia 1-5	
10:20	Coffee	
11:00	Symposia 1-5 continued	
12:40	Lunch	(ESEB Council Meeting)
14:00	Symposia 1-5 continued	
15:20	Tea	
16:00	Symposia 1-5 continued	
17:30	Poster session for Symposia 1-15	
18:30	Discussion on 'Open Access Publishing'	
19:30	Dinner	
18:00 – 23:59	Terrace Bar open, Leeds University Union	

Wednesday 20 August

08:50	Plenary	Daniel Hartl Evolutionary Genomics: Platform for a New Modern Synthesis
	Chair	Godfrey Hewitt
09:50	Symposia 6-10	
10:20	Coffee	
11:00	Symposia 6-10 continued	
12:40	Lunch	(JEB Editorial Board Meeting)
14:00	Symposia 6-10 continued	
15:20	Tea	
16:00	Symposia 6-10 continued	
17:30	Tea	(JEB Deciding Editors Meeting)
18:00	Presidential address	Rolf Hoekstra
18:40	Maynard Smith Prize lecture	Patricia Beldade
19:30	Dinner	

18:00 – 23:59 Terrace Bar open, Leeds University Union

Thursday 21 August

08:20	Plenary	Paul Brakefield Butterfly eyespots and the power of evo-devo to explore evolutionary constraints
	Chair	Peter van Tienderen
09:20	Symposia 11-15	
10:20	Coffee	
11:00	Symposia 11-15 continued	
12:40	ESEB Business Meeting	
13:10	Lunch	
14:00	Excursions depart from Parkinson Steps	

Posters for Symposia 1-15 should be removed before the coffee break.
Posters for Symposia 16-30 can be put up from lunch time onwards.

Friday 22 August

08:20	Plenary	Allen Orr The genetics of adaptation: What do we know?
	Chair	Nicholas Barton
09:20	Symposia 16-20	
10:20	Coffee	
11:00	Symposia 16-20 continued	
12:40	Lunch	
14:00	Symposia 21-25 continued	
15:20	Tea	
16:00	Symposia 21-25 continued	
17:30	Poster session for Symposia 16-30	
20:00	Reception and Congress Dinner	Royal Armouries Museum

Saturday 23 August

08:50	Plenary	Robert Wayne Conservation genetics in the new molecular age
	Chair	Richard Nichols
09:50	Symposia 26-30	
10:20	Coffee	
11:00	Symposia 26-30 continued	
12:40	Lunch	
14:00	Symposia 26-30 continued	
15:20	Tea	
16:00	Symposia 26-30 continued	

18:00 – 23:59 Terrace Bar open, Leeds University Union

Plenary talks

Conference Auditoria 1 & 2 (video-linked)

Tuesday

EVOLUTION AND EVERYDAY LIFE: EXAMPLES OF RELEVANCE AND NEGLECT

Robert M May

Zoology Department, University of Oxford, Oxford OX1 3PS, UK

Under this grandiose heading I plan to talk about a wide range of policy-relevant issues where evolutionary considerations are usually given inadequate attention: evolution of resistance in both medical and agricultural contexts; evolution of exploited populations under harvesting; evolution of virulence; the relevance of population genetics, and other evolutionary considerations, as complicating factors against the glib generalisations about "post-genomics"; and – perhaps most important but running the risk of degenerating into waffle – the many ways in which our continuing failure to understand how cooperative behaviour may evolve and persist (probably connected to other unanswered questions in the evolution of language) greatly impedes efforts to come to collective decisions about topics as varied as stem cell research, GM crops, MMR vaccination, and ultimately the reconciling of collective interests with individual interests.

Wednesday

EVOLUTIONARY GENOMICS: PLATFORM FOR A NEW MODERN SYNTHESIS

Daniel L. Hartl, Jose M. Ranz, Cristian I. Castillo-Davis and Colin D. Meiklejohn

Harvard University, Cambridge, Massachusetts

Many genes associated with male reproduction are known to evolve rapidly in amino acid sequence. We have carried out transcription profiling by means of cDNA microarrays to detect polymorphism in gene expression among approximately 5000 genes in *Drosophila*. Among eight strains of *D. melanogaster*, 45% of the genes showed significant expression differences between males of at least one pair of strains, whereas 5% are expected by chance. This result indicates that at least 40% of the genome is differentially regulated between males in populations of *D. melanogaster*. Among the genes that show variation in expression, genes that are male-biased in their expression are overrepresented and those that are female-biased are underrepresented. A strong effect of sex-dependent expression is also observed in the divergence between the sibling species *D. melanogaster* and *D. simulans*. While ~50% of the transcriptome has evolved differences in expression, ~83% of these differences involve an increase, decrease, gain, loss or reversal of sex-biased expression. Male-biased genes show greater divergence than female-biased genes. These results suggest that selection affecting male-biased genes may drive changes in expression of many of the most rapidly evolving genes in *Drosophila*.

Thursday

BUTTERFLY EYESPOTS AND THE POWER OF EVO-DEVO TO EXPLORE EVOLUTIONARY CONSTRAINTS

Paul M. Brakefield

Institute of Biology, Leiden University, PO Box 9516, 2300 RA Leiden, The Netherlands

Few would find the idea that evolutionary constraints on phenotypic change **could** play a role in shaping patterns of morphological stasis or adaptive radiation controversial. The problem lies more in a lack of rigorous data to help extend the discussion of the concept of constraints beyond conjecture. I will illustrate how a combination of evolutionary developmental biology ('evo-devo') and evolutionary genetics can provide the background to exploring generative constraints: How do the properties of the genetical and developmental mechanisms that generate variation in the phenotype influence the tempo and direction of evolutionary change? The formation of eyespots on the wings of the African butterfly, *Bicyclus anynana*, is a developmental process which is becoming comparatively well known. We also examine how physiological mechanisms underlie phenotypic plasticity and life history traits in this system. Artificial selection experiments provide us with a major tool to explore the genetic variances and co-variances underlying evolutionary responses in different directions of phenotypic change. The descriptions of the genetic variation in combination with analyses of the ways in which developmental and physiological pathways are modulated in the course of selection may then provide insights about potential generative constraints. Some recent work emphasizes that careful experimental design is necessary to be able to make robust interpretations. Being able to map phenotypes onto genotypes via developmental processes provides a powerful basis for beginning to explore one type of potential evolutionary constraint so that the concept can be treated in the future as something more than another 'just-so' story.

Friday

THE GENETICS OF ADAPTATION: WHAT DO WE KNOW?

H. Allen Orr

University of Rochester, New York

Although nearly all evolutionists think that adaptation drives phenotypic evolution, evolutionary theory has had almost nothing to say about adaptation. The result is a curious disconnect between the verbal theory of neo-Darwinism and the mathematical theory of evolution. The rise of QTL and experimental evolution approaches has made this disconnect particularly clear: we can make almost no theoretical predictions about what should be seen in such experiments. I review the historical reasons for this neglect of adaptation as well as recent attempts to construct a true mathematical theory of adaptation. Along the way, I consider how a theory of adaptation differs from a theory of natural selection.

Saturday

CONSERVATION GENETICS IN THE NEW MOLECULAR AGE

Robert K. Wayne

Department of Organismic Biology, Ecology and Evolution, University of California at Los Angeles, Los Angeles, California U.S.A. 90095-1606.

Conservation genetics has entered a new age in which a tremendous range of genomic resources are available to categorize diversity at multiple evolutionary levels from the kinship of individuals to relationships of populations and species. Further, genetic diversity of neutral markers can now potentially be contrasted with that of genes influencing fitness. Molecular genetic studies increasingly incorporate information on phenotype, behavior, geologic history and ancient DNA to explain patterns of evolutionary divergence. A synthesis of information from ecology, behavior and genetics is needed in the diagnosis of endangered species to better conserve pattern and process and improve the probability that species will survive into the future. I discuss the problems that have plagued past conservation genetic assessments of endangered species and provide example of new more integrative approaches that may lead to more effective conservation and management.

John Maynard Smith Prize lecture

THE GENETIC BASIS OF PHENOTYPIC VARIATION: EVOLUTION AND DEVELOPMENT OF BUTTERFLY WING PATTERNS

Patrícia Beldade

Ecology and Evolutionary Biology, University of California at Irvine

Heritable phenotypic variation is the "raw material" of evolution by natural selection, and understanding the mechanisms that generate such variation has become a fundamental challenge for contemporary evolutionary biology. In recent years, evolutionary developmental biology has encouraged a change of focus from the sorting of phenotypic variation by selection to the production of that variation through development. The colour patterns decorating butterfly wings provide ideal material to study the reciprocal interactions between evolution and development in this process. They are visually compelling products of selection, often with a clear adaptive value, and are also amenable to a detailed developmental characterization at different levels. We studied different aspects of the process of generation of variants in *Bicyclus anynana* eyespot patterns. Results will be discussed of experiments where we have used artificial selection to explore the potential for changes in eyespot size phenotypes, which were thought to be constrained by the properties of butterfly wing pattern development. We also report on experiments aimed at identifying the actual genes involved in the response to selection. Our results show that a combination of approaches from evolutionary and developmental biology used to study the patterns of colour on butterfly wings can greatly contribute to understanding how evolutionarily relevant variation is generated.

Symposium 1: JEB Special Symposium:
The role of evolutionary biology in understanding, preventing and treating infectious diseases
Organiser: Bruce Levin

Conference Auditorium 1

09.50 – 10.20	**Lipsitch, M.** Antibiotic use and resistance: An evolutionary / population perspective
10.20 – 11.00	**Coffee**
11.00 – 11.30	**Andersson, D. I.** Adapting to the deleterious effects of antibiotic resistance
11.30 – 12.00	**Baquero, F.** Antibiotic Resistance: Adapting to adversity by manipulating mutation rates and local tool-box genetic resources
12.00 – 12.30	**Peck, S. L.** The spread of antibiotic resistance in a spatially structured hierarchy of metapopulations
12.30 – 14.00	**Lunch**
14.00 – 14.30	**Gupta, S.** The effects of immune selection on the population dynamics of malaria
14.30 – 15.00	**Svanborg, C.** Genetic control of innate immune responses and resistance to kidney infection: some evolutionary implications
15.00 – 15.30	**Hambuch, T. M.** Evolutionary Genetics of Smallpox
15.30 – 16.00	**Tea**
16.00 – 16.30	**Reece, S. E.** Host anaemia and sex ratios in malaria parasites
16.30 – 17.00	**Day, T.** A general theory for the evolutionary dynamics of virulence
17.00 – 17.30	**Dionisio, F.** Evolution of conjugative plasmids under antibiotic pressure
17.30 – 17.40	**Levin, B.** Summary and overview

Invited Talks

1.1

ANTIBIOTIC USE AND RESISTANCE: AN EVOLUTIONARY / POPULATION PERSPECTIVE

Marc Lipsitch

Department of Epidemiology, Harvard School of Public Health

Antimicrobial agents (antivirals, antibacterials, and antiparasitic drugs) are the cornerstone of infectious disease treatment. From a medical perspective, the primary goal is to cure an individual patient. From a population (public health) perspective, treatment has two additional effects: for some infections, treatment is a major means of preventing transmission of infection to other people, and for nearly all infections, treatment, by exerting selection for resistant strains, puts other people at risk of acquiring infections that will be harder and more expensive to treat. Given these considerations, ideal use of antimicrobial drugs (antibiotics for short) would: 1) cure the most patients at the lowest cost; 2) reduce transmission as much as possible; and 3) minimize selection for resistant strains. How to balance these goals is a formidable problem for applied evolutionary biology / microbial ecology. After a brief discussion of these problems in gloriously abstract terms, a particular case study will be considered in more detail: antibiotic resistance in *Streptococcus pneumoniae*. Using a combination of epidemiological data analysis, mathematical models of transmission, and laboratory studies, I will describe several of the key factors influencing the patterns of evolution of resistance. Specifically, I will consider the interaction between the immune system and antibiotics in natural selection of strains of *S. pneumoniae*, the role of antibiotic use in promoting resistance, and the source of spatial variation in levels of resistance. Other topics in the evolution of resistance will be touched on as time allows.

1.2

ADAPTING TO THE DELETERIOUS EFFECTS OF ANTIBIOTIC RESISTANCE

Dan I. Andersson

Swedish Institute for Infectious Disease Control, Dept. of Bacteriology Nobels vg 18, S-171 82 Stockholm, Sweden

Sixty years of use and misuse of antibiotics has resulted in increased frequencies of resistance for almost every combination of antibiotic and bacteria. This bacterial adaptive evolution has been so successful that today some bacterial infections are nearly untreatable with antibiotics, generating considerable medical problems. Even though most drug resistances confer a fitness cost on the bacteria, suggesting that they might disappear by reducing the volume of antibiotic use, increasing experimental evidence indicate that several processes will act to cause long-term persistence of the resistant bacteria. Compensatory evolution that reduces or eliminates the costs of resistance, the presence of cost-free resistance mechanisms and genetic hitch-hiking between non-selected and selected resistances will all act to confer a stabilisation of the resistant bacteria. Thus, if antibiotic resistant bacteria have ascended to a high frequency in the community they will probably remain there for a long time. These results emphasize the need for long-term strategies to reduce resistance development to prolong the useful lifespan of our available antibiotics.

1.3

ANTIBIOTIC RESISTANCE: ADAPTING TO ADVERSITY BY MANIPULATING MUTATION RATES AND LOCAL TOOL-BOX GENETIC RESOURCES

FERNANDO BAQUERO

Department of Microbiology, Ramón y Cajal University Hospital, 28034 Madrid, Spain.

The frequency of antibiotic resistance among bacterial pathogens is very heterogeneous in different clinical situations and geographical places. Differences can be explained in part because of the different intensities of antibiotic selection. But selection is dependent on the availability of selectable characters offered by bacterial variation. In different situations and places, the wealth of genetic variability may differ, and so the frequency of resistance. In *Pseudomonas aeruginosa*, the frequency of strong, but also of weak hyper-mutable isolates is very frequent in cystic fibrosis patients, and many of these strains behave as multiresistant when confronted to antibiotics. In *Escherichia coli*, if the proportion of strong mutators is around 1% in Spain, but the frequency of weak mutators (mutation frequency between 5E-8 and 5E-7) reach 19 % among urinary pathogens, 29 % among blood isolates, and 32 % in strains harboring extended-spectrum beta-lactamases. These data illustrate the presence of a frequent latent potential for mutational antibiotic resistance in the local populations. Moreover, we show that a number of antibiotics increase the mutation frequencies by inducing the expression of error-prone polymerases. Analyzing long series (10 or more years) of resistant isolates in our hospital, as well as strains from healthy volunteers and animals, we suggest that differences in antibiotic resistance frequencies in different locations also depends on the local availability not only of resistance genes, but also of gene-capture units (as integrons), genetic elements involved in horizontal gene transfer, and particular bacterial clones of high efficiency of spread, that contribute to the broad dissemination of all these elements. Different local combinations of genetic traits, tools and vehicles extracted from a common pool in particular places give rise to different evolutionary outcomes adapting microorganisms to adversity.

1.4

THE SPREAD OF ANTIBIOTIC RESISTANCE IN A SPATIALLY STRUCTURED HIERARCHY OF METAPOPULATIONS

Steven L. Peck

Department of Integrative Biology, Brigham Young University,Provo, UT, 84602, USA

Spatial scale strongly affects the evolution of antibiotic resistance. Resistance is known to spread at several spatial scales: among families, among hospital patients, within a community, among different communities, and even across large regions. Here I examine a finite population stochastic interaction network model implemented using Mathematica and C++. This metapopulation model looks at the effect of differential selection regimes on the regional spread of resistance. The model explores a nested spatial hierarchy of metapopulations. Each level contains subpopulations of individuals that move among other subpopulations at the same level with probability proportional to proximity. Subpopulations at the lowest level of the hierarchy represent locally interacting individuals such as those that might be found in a hospital, or individuals in a common workplace, or even members of a single neighborhood. The next level in the hierarchy represents local clusters of such subpopulations. Higher levels in the hierarchy represent regional movement. At the lowest level, each individual subpopulation is under a subpopulation-specific selection regime imposed by antibiotic use. Within a single individual, antibiotic resistance is modelled with simple deterministic equations. The model shows how antibiotic resistance develops under such hierarchal spatial structuring and looks at the effect of various management practices on reducing antibiotic resistance.

1.5

The effects of immune selection on the population dynamics of malaria

Sunetra Gupta

University of Oxford

I will discuss how mathematical models can help us understand the emergence and maintenance of antigenic diversity in *P. falciparum*. Simple models demonstrate that immune selection by the host can cause pathogen populations to self-organise into non-overlapping combinations of antigenic variants, which may function at an epidemiological level as independently transmitted strains. I will show how this theoretical framework can be used to intrepret patterns of infection and disease and the molecular epidemiology of *P. falciparum* malaria. I will also show immune selection can influence the dynamics of infection within a single host, and present a new hypothesis regarding antigenic variation which provides a new solution to the conundrum of how pathogens achieve a sequential, rather than simultaneous, appearance of the immunologically distinct variants.

Contributed talks

1.6

Genetic control of innate immune responses and resistance to kidney infection: Some evolutionary implications

[1]Ann-Charlotte Lundstedt, [2]Shane McCarthy, [1]Gabriela Godaly, [3]Diana Karpman, [1]Irene Leijonhufvud, [1]Martin Samuelsson, [1]Patrik Samuelsson, [1]Majlis Svensson, [2]Bjrn Andersson, [1]**Catharina Svanborg**

[1]*Department of Microbiology, Immunology and Glycobiology, Division of Laboratory Medicine, Lund University, Slvegatan 23, S-223 62 Lund, Sweden;*

[2]*Department of Genetics and Pathology, Center for Genomics and Bioinformatics, Karolinska Institutet, Stockholm, Sweden;*

[3]*Department of Paediatrics, Lund University, Lund, Sweden.*

Urinary tract infections are clustered in certain individuals, but the molecular basis of disease susceptibility remains unknown. Two steps control the host response. 1. Receptors for bacterial fimbriae and Toll receptors determine how the mucosa will respond to infection, and if the bacteria will or will not break the inertia of the mucosal barrier. This step distinguishes asymptomatic carriage from symptomatic infection. Thus, hosts with defects in toll receptor or fimbrial receptors are protected from developing symptomatic infection. 2. The responding epithelial cells produce chemokines that recruit neutrophils to the mucosa and direct them across the barrier and into the lumen. These are the crucial effector cells involved in bacterial clearance. Recently, mIL-8Rh knock-out mice were shown to develop the entire syndrome of acute pyelonephritis and renal scarring, with neutrophil trapping in infected kidneys. This mechanism is implicated also in human disease, as pyelonephritis-prone patients showed reduced expression of CXCR1; a human IL-8 receptor. CXCR1 sequencing revealed heterozygous polymorphisms in 38% of the patients, but not in age-matched controls. The single nucleotide polymorphisms (SNPs) potentially changed transcription factor specificity or polyadenylation, suggesting a possible link to gene expression. CXCR1 SNPs may thus render individuals pyelonephritis-prone by lowering CXCR1 expression and impairing neutrophil function. The evolutionary advantage associated with asymptomatic carriage and toll receptor mutations and the disadvantage of SNPs in CXCR1 will be discussed.

1.7

Evolutionary genetics of smallpox

[1]**Tina M. Hambuch**, [1]Chris Schmidt, [1]Mike Frace, [1]Melissa Olsen-Rasmussen, [2]Scott Sammons, [2]Ming Zhang, [2]John Osborne, [2]Inger Damon [2]Russell Regnery

[1]*Dept. Biologie II der LMU, Luisenstrasse 14, 80333 Munich, Germany*

[2]*Centers for Disease Control, Atlanta GA 30308, USA*

Variola virus, the agent of smallpox, is unusual among chorodopoxviruses for its decreased genome size and its host specificity. We had access to thirty five strains of variola virus collected over thirty years from various geographic sites. Forty genes, sampled across the entire genome and representing a variety of functions, were sequenced for all of these strains. Standard population genetic measures were used to assess genetic diversity and evidence of differentiation among the strains. Further, molecular evolutionary methods were used to assess selective pressures on genes. Using this combination of methods, we were able to identify trends in specific strains of this virus as well as identify trends across genes and gene regions.

1.8

HOST ANAEMIA AND SEX RATIOS IN MALARIA PARASITES

Sarah E Reece, Stuart A West, Andrew F Read

University of Edinburgh, ICAPB, West Mains Road, Edinburgh, EH93JT

Malaria and other haemosporin parasites must undergo a round of sexual reproduction in their vector in order to transmit to new hosts. Consequently, it is crucial that parasites produce the sex ratio (proportion of male) that will maximise transmission to new hosts. There is some evidence to show that, consistent with evolutionary theory, the sex ratios of malaria parasites are negatively correlated to their inbreeding rate and this relationship has provided a broad scale understanding of protozoan sex ratios. However, observed sex ratios and those most infective to mosquitoes can be less female-biased than theory predicts. Recent evidence implies that malaria sex ratios increase with the host's anaemic response, and this is a facultative response to maintain transmission success. We investigated the roles that host anaemia, erythropoesis and nitric oxide play in shaping both the investment in sexual stages and the sex ratio in the rodent malaria parasites *Plasmodium chabaudi* and *Plasmodium vinckei.*

1.9

A GENERAL THEORY FOR THE EVOLUTIONARY DYNAMICS OF VIRULENCE

[1]**Troy Day,** [2]Steve Proulx

[1]*Jeffery Hall, Queen's University, Kingston, ON, K7L 3N6, CANADA*

[2]*University of Oregon*

Most theory on the evolution of virulence is based on a game-theoretic approach. One potential shortcoming of this approach is that it does not allow the prediction of the evolutionary dynamics of virulence. Such dynamics are of interest for several reasons: for experimental tests of theory, for the development of useful virulence management protocols, as well as for understanding virulence evolution in situations where the epidemiological dynamics never reach equilibrium and/or when evolutionary change occurs on a time scale comparable to that of the epidemiological dynamics. Here we present a general theory similar to that of quantitative genetics in evolutionary biology that allows for the easy construction of models that include both within-host mutation as well as superinfection, and that is capable of predicting both the short- and long-term evolution of virulence. We illustrate the generality and intuitive appeal of the theory through a series of examples, and show how it leads to transparent interpretations of the selective forces governing virulence evolution. It also leads to novel predictions that are not possible using the game-theoretic approach.

1.10

EVOLUTION OF CONJUGATIVE PLASMIDS UNDER ANTIBIOTIC PRESSURE

Francisco Dionisio, Inês C. Conceição, Ana C. Marques, Isabel Gordo

Instituto Gulbenkian de Ciencia, Rua da Quinta Grande, 6, Apartado 6, P-2781-901-Oeiras, Portugal

Previous reports have shown that, although plasmids confer a fitness cost to their bacterial hosts, a few hundreds of generations under antibiotic pressure may suffice for the pair cell + plasmids to co-adapt. That is, plasmid-bearing cells evolve such that their fitness becomes similar to that of plasmid-free cells in the absence of antibiotics. These previous studies focused on the evolution of non-conjugative plasmids. I am going to present experimental results concerning the evolution of a conjugative plasmid under antibiotic pressure. In particular, I am going to discuss the transfer ability, fitness cost and resistance to antibiotics of the evolved plasmid and compare to that of the ancestral plasmid. Finally, I'll discuss the importance of our results to public health.

Posters

1.11P

HOST GENOTYPE AFFECTS WITHIN-HOST COMPETITION BETWEEN RODENT MALARIA PARASITES

J. C. De Roode, S. Cheesman, R. Culleton, R. Carter, A. F. Read

Institute of Cell, Animal and Population Biology, University of Edinburgh, Kings Buildings, West Mains Road, Edinburgh EH9 3JT, Scotland, UK

As with other organisms, malaria parasites compete for limited amounts of food, mates and space. Different parasites infecting the same host, for example, face competition for limited numbers of red blood cells. Competition affects parasite growth rate, transmission, and virulence, and is thus important for parasite evolution. Theory predicts that virulent clones outgrow avirulent ones, leading to the evolution of higher virulence. We infected laboratory mice with a mixture of two *Plasmodium chabaudi* clones: one virulent, the other avirulent. Using quantitative real-time PCR, we indeed found that the virulent clone overgrew the avirulent clone. However, whereas in one mouse strain the avirulent clone disappeared below detectable levels, in another strain it was only suppressed, and returned to overgrow the virulent clone later on during the infection. We suggest these differences may be explained by different immune responses to the two parasite clones in different mouse strains. Host immune status therefore seems an important factor in within-host competition between parasite clones and the evolution of parasite virulence.

1.12P

EVOLUTION OF MULTIHOST PARASITES

S. Gandon

CEPM, IRD, 911 avenue Agropolis 34394 Montpellier, France

Many parasites can infect different types of hosts or even different host species. Epidemiological models have shown the importance of the diversity of potential hosts to understand the dynamics of infectious disease (e.g. the importance of reservoirs) but the evolutionary consequences of this diversity remain largely overlooked. Here, I present a general theoretical framework for the study of life history evolution of multihost parasites. In particular, this analysis shows how evolution depends on epidemiology (the relative abundance of different types of infected hosts) and on between-trait constraints (both within and between different types of hosts). I illustrate these effects in different situations under the simplifying assumption that parasites can infect only two types of hosts. These simple but contrasted evolutionary scenarios yield new insights into virulence evolution and on the evolution of complex life cycles. The possible implications of these results for the management of pathogen dynamics and evolution are discussed.

1.13P

INSECTS AND BACTERIA VERSUS MAN: WHO IS FASTER IN THE EVOLUTIONARY ARMS RACE?

Tamar Keasar

Achva College, Mobile Post Shikmim 79800, Israel

The recent histories of human combat with insect pests and with microbial pathogens show many parallel developments. Both fields were revolutionized by the discovery of new chemical control agents (DDT and Pencillin) in the 1940s, followed by the rapid development of many other chemical insecticides and antibiotics. Misuse and overuse of insecticides and antimicrobials resulted in common problems, including selection for resistant (often multiply-resistant) genotypes; suppression of harmless or beneficial non-target organisms; population increases of new harmful species; and adverse side effects on humans. In spite of heavier selection pressures, shorter generation times, and widespread horizontal transmission of antimicrobial resistance, bacteria were slower to acquire resistance to chemicals than insects. Possibly, the rarity of sexual reproduction in bacteria, as compared to insects, can explain their slower rates of evolution. Scientific and public concern over the detrimental ecological effects of insecticides led to the development of Integrated Pest Management strategies. It is hypothesized that similar strategies can be used sustainably to manage bacterial communities. A literature survey reveals increasing efforts to develop methods for resistance control, cultural and biological control of bacterial pathogens. Tighter interactions between entomologists and medical researchers are expected to yield fruitful insights into this important issue.

Symposium 2

Reproductive parasites in evolution

Organisers: Greg Hurst & Tim Karr

Conference Auditorium 2

09.50 – 10.20	**Jiggins, F.** Host-parasite coevolution between sex ratio distorting microbes and their hosts
10.20 – 11.00	**Coffee**
11.00 – 11.30	**Breeuwer, J. A. J.** Haploid female parthenogenesis in the mite *Brevipalpus phoenicis* is caused by a new bacterium
11.30 – 12.00	**Bazinet, C.** The Cellular Archeology of Sex
12.00 – 12.20	**Ubeda, F. F. U.** Why Mendelian segregation?
12.20 – 12.40	**Burt, A.** Site-specific selfish genes as tools for the control and genetic engineering of natural populations
12.40 – 14.00	**Lunch**
14.00 – 14.20	**Rigaud, T.** Consequences of Wolbachia-induced female biased sex ratios on their isopod host reproductive success
14.20 – 14.40	**Reuter, M.** Loss of Wolbachia infection during colonisation in the invasive Argentine ant *Linepithema humile*
14.40 – 15.00	**Tinsley, M.** Host specificity of male-killing bacteria in ladybirds
15.00 – 15.20	**Pannebakker, B.A.,** Cytology of *Wolbachia* induced parthenogenesis in *Leptopilina clavipes* (Hymenoptera: Figitidae)
15.20 – 16.00	**Tea**
16.00 – 16.20	**Egas, M.** Evolution of incompatibility types in CI Wolbachia is structurally unstable under the mod-resc hypothesis
16.20 – 16.40	**Butcher, R. D. J.** Competition and co-operation between intracellular insect symbionts within a common host
16.40 – 17. 00	**Perrot-Minnot, M.-J.** Castration of intermediate hosts by acanthocephalan parasites : adaptive trait or by-product of manipulation
17.00 – 17.20	**Smith, J. E.** The evolutionary origins of vertical transmission in microsporidian parasites

Invited talks

2.1

HOST-PARASITE COEVOLUTION BETWEEN SEX RATIO DISTORTING MICROBES AND THEIR HOSTS

Francis Jiggins

Department of Genetics, University of Cambridge, Downing Street, CB2 3EH, UK

An evolutionary conflict exists between hosts, which are selected to become resistant to parasites, and parasites, that are selected to evade those host defences. The resulting host-parasite coevolution can take two forms. First, an evolutionary arms race may develop in which successive novel adaptations are fixed in the host and parasite populations. Second, gene for gene type coevolution can result in balancing selection maintaining multiple host and parasite genotypes in the population. I will explore the role these processes have played in the evolution of microbial sex ratio distorters in insects.

2.2

HAPLOID FEMALE PARTHENOGENESIS IN THE MITE *BREVIPALPUS PHOENICIS* IS CAUSED BY A NEW BACTERIUM

[1]**Johannes A.J. Breeuwer**, [2]Andrew R. Weeks

[1]*University of Amsterdam, The Netherlands*

[2]*La Trobe University, Australia*

It had previously been thought that no species within the animal kingdom lives exclusively in a haploid state. While haplodiploidy (haploid males and diploid females) has evolved many times within animals, haploid females have never been found. However, in the early 1980's, a group of dutch cytogeneticists, while studying chromosome evolution within the economically important mite superfamily, the Tetranychoidea, proposed that they had found the first animal species that existed exclusively within the haploid state. We provide the evidence needed to show that *B. phoenicis* does indeed live entirely in a haploid state. We also discovered that feminization and parthenogenesis is caused by a new undescribed bacterium from the Cytophaga-Flavobacterium-Bacteroides (CFB) phylum. A preliminary survey suggests that this bacterium infects other arthropod and nematode hosts and can co-occur with *Wolbachia* in a single host. These findings raise several questions about current research into endosymbionts, including *Wolbachia*, that have been presumed to cause various phenomena within their hosts.

2.3

THE CELLULAR ARCHEOLOGY OF SEX

Chris Bazinet

Department of Biological Sciences, St. John's University, Jamaica, NY 11439, USA

Close examination of the specialized cellular mechanisms of the germ line may offer instructive clues to the evolutionary origins of sex. The extraordinary dynamics of mitochondria in both male and female germ cells have generally been considered to be the consequence of the presumably large energy requirements of germ cell morphogenesis and motility, and of the need to ensure transmission of healthy mitochondria to the next generation. An alternative hypothesis is proposed, in which the germ line life cycle is descended from the life cycle of the endosymbiotic ancestor of mitochondria. Mitochondrial dynamics in *Drosophila* sperm individualization are strikingly reminiscent of the actin-based "comet tail" motility employed by a number of intracellular microbes including *Listeria, Shigella,* and *Rickettsia* of the Spotted Fever Group (SFG). The close relatedness of mitochondria to the Rickettsiaceae is consistent with a common evolutionary derivation of SFG and mitochondrial actin-based motility. A distinctive feature of SFG rickettsia is the high frequency with which they are seen moving within the nucleus of infected cells, providing an opportunity for interaction with the host genome. Following ingestion of, or entanglement with, host DNA during this "nuclear phase", a motile SFG rickettsia could potentially carry genes from one host cell to another. In this sense, the original sperm or protosperm is proposed to have been a common ancestor of mitochondria and the SFG rickettsia. The actin-based motility of this organism could provide a linkage between primitive forms of nuclear gene segregation, cytoplasmic reorganization, and cell-cell interactions that are proposed to have coevolved to become the meiosis, gametogenesis, and fertilization, respectively, of the contemporary germ cell life cycle. The hypothesis of a Rickettsial/mitochondrial origin of sex rationalizes a number of surprising and otherwise unexpected observations of mitochondrial participation in critical germ cell functions, as well as providing a theoretical basis for the extraordinary capacity of *Wolbachia,* another close mitochondrial relative, to manipulate germline pathways. If mitochondria are providing numerous morphogenetic functions within germ cells, a close relative should be best equipped to compete with or co-opt these mitochondrial functions.

Contributed talks

2.4

WHY MENDELIAN SEGREGATION?

Francisco Ubeda, David Haig

Organismic and Evolutionary Biology Department. Harvard University. 26 Oxford St. Cambridge, MA 02138, USA

According to Mendelian laws of inheritance, the alleles at an autosomal locus of a diploid organism are equally represented among its gametes. However, segregation distorters violate fair meiosis by sabotaging some of their competing homologues thereby being transmitted to more than their fair share of offspring. The evolution of the segregation ratio has been modeled using two-locus models. The modifier locus determines distortion strength (the fraction of gametes carrying the driving allele) while the main locus determines genotype viability. If the recombination rate between the two loci is less than ½, Mendelian segregation is vulnerable to subversion by segregation distorters but it is immune if the recombination rate is equal to ½. These models are critically limited because distortion strength is assumed to be equal in males and females, despite the fact that all known systems of meiotic drive involve distortion in one sex only. That is the case of the t-haplotype in mouse and the Segregation Distorter in Drosophila in which the segregation ratios are 0.9 to 0.99 in males and 0.5 in females. Our work starts at the point where Eshel left off introducing sex-specific segregation distortion as well as differential fitness of reciprocal heterozygotes. Whereas Eshel concludes that free recombination stabilizes Mendelian segregation, our results indicate that even in this case Mendelian segregation is susceptible to invasion by some modifiers of the segregation scheme. The outcome of this research opens up a fundamental question: if Mendelian segregation is unstable, why is it the form of segregation present in most living organisms?

2.5

SITE-SPECIFIC SELFISH GENES AS TOOLS FOR THE CONTROL AND GENETIC ENGINEERING OF NATURAL POPULATIONS

Austin Burt

Imperial College, Silwood Park, Ascot, SL5 7PY, UK

Some species – a relatively small number – cause substantial harm to the human condition; most prominent are those that cause disease, transmit disease, or reduce agricultural output. Here I investigate the possibility of controlling these species by use of site-specific selfish genes (homing endonuclease genes, group II introns, and LINEs). Computer simulations show that if such genes can be engineered to target new host sequences, then they can be used to manipulate natural populations, even if the number of individuals released is a small fraction of the entire population. For example, a genetic load sufficient to eradicate a population can be imposed in less than 20 generations, if the target is an essential host gene, the knock-out is recessive, and the selfish gene has an appropriate promoter. There will be selection for resistance, but several strategies are available for reducing the likelihood of it evolving. These genes may also be used to genetically engineer natural populations, including population-wide gene knock-outs, gene replacements, and genetic transformations. By targeting sex-linked loci just prior to meiosis one may skew the population sex ratio, and by changing the promoter one may limit the spread of the gene to neighbouring populations. The proposed constructs are evolutionarily stable in the face of the mutations most likely to arise during their spread, and strategies are also available for reversing the manipulations.

2.6

CONSEQUENCES OF WOLBACHIA-INDUCED FEMALE BIASED SEX RATIOS ON THEIR ISOPOD HOST REPRODUCTIVE SUCCESS

[1]**Thierry Rigaud**, [2]Jérôme Moreau

[1]Université de Bourgogne, Equipe Ecologie Evolutive, 6 Bd Gabriel, 21000 Dijon, France

[2]Université de Poitiers, UMR CNRS 6556, 40 Av du Recteur Pineau, 86022 Poitiers Cedex, France

Intracytoplasmic symbionts may gain transmission to a new host generation via female eggs but not male sperm. Bacteria of the genus *Wolbachia* are a typical example. They infect a large range of arthropod species and manipulate host reproduction in several ways. These two characteristics led to the assumption that they may have important consequences on host evolutionary biology. While direct consequences begin to be well known, all indirect consequences of host reproduction manipulation have not been investigated yet. In terrestrial isopods (woodlice), *Wolbachia* are responsible for converting males into females (feminisation) in some species, and impose a strong excess of females on their host populations. This talk will be about the consequences of this sex ratio bias on host reproductive strategies (potential rate of reproduction, competition for mate), and about the potential feed back these consequences may have on parasite success. We show that males of isopod hosts harbouring feminising *Wolbachia* possess a strong mating capacity (i.e. are able to mate with several females in a short time), while those of species harbouring non feminizing *Wolbachia* possess a weaker mating capacity. This pattern may be explained by the selection of high mating capacity following the increase in female-biased sex ratios. On the other hand, isopod males facing an excess of females chose more often uninfected females as sexual partner than *Wolbachia*-infected females. This choice is not a direct consequence of the infection, but is rather due to the fact that infected females are genetic males sexually reversed by the parasite. In addition, males provide less sperm to the infected females they inseminate. This difference in sperm number may affect the infected female fertility, but only in a context of sperm depletion. Consequences of these findings on the parasite success in natural host populations are discussed.

2.7

LOSS OF *WOLBACHIA* INFECTION DURING COLONISATION IN THE INVASIVE ARGENTINE ANT *LINEPITHEMA HUMILE*

[1]**Max Reuter,** [2]Jes S. Pedersen, [1]L. Keller

[1]University of Lausanne, IE-ZEA, Bâtiment de Biologie, 1015 Lausanne, Switzerland

[2]Department of Population Ecology, Zoological Institute, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark

Wolbachia are maternally inherited bacteria which are very common in arthropods and nematodes. *Wolbachia* infection may affect host reproduction through feminization, parthenogenesis, male-killing, cytoplasmic incompatibility and increased fecundity. Previous studies showing discrepancies between the phylogenies of *Wolbachia* and its arthropod hosts indicate that infection is frequently lost, but the mechanisms of symbiont extinction have so far remained elusive. Here, we report data showing that colonisation of new habitats is a possible mechanism leading to the loss of infection. The presence and prevalence of *Wolbachia* were studied in two native and eight introduced populations of the Argentine ant *Linepithema humile* as well as one population of a closely related species (*Linepithema*).

2.8

HOST SPECIFICITY OF MALE-KILLING BACTERIA IN LADYBIRDS

Matt Tinsley

Department of Genetics, University of Cambridge, Downing Street, CB2 3EH

The evolutionary origins of the symbioses between maternally inherited bacteria that manipulate arthropod reproduction and their host species are currently unclear. Whilst some closely related insects are infected by closely related symbionts, some distantly related hosts also share relatively similar bacteria. Artificial microinjection of *Wolbachia* and other symbionts between *Drosophila* species has suggested that bacteria could transfer with relative ease between different hosts. However, reports of successful experimental trans-infection between different genera are rare. We have investigated the host specificity of the male-killing *Spiroplasma* bacterium from the two spot ladybird, *Adalia bipunctata*, by injecting it into a range of other ladybird species. Transfer to the native host and the con-generic ten spot ladybird had perfect success, resulting in 100% transmission. In species outside the *Adalia* genus, infection established less frequently and the male-killing trait varied in penetrance. Characteristics of novel infections ranged from causing total mortality of both male and female embryos, to a reduced ability to kill males. These studies suggest that phylogenetic constraints exist for the horizontal movement of male-killers on an evolutionary timescale. In addition they shed light on the potential mechanisms by which host resistance to these bacteria might evolve.

2.9

CYTOLOGY OF *WOLBACHIA* INDUCED PARTHENOGENESIS IN *LEPTOPILINA CLAVIPES* (HYMENOPTERA: FIGITIDAE)

[1]**Bart A.Pannebakker**, [2]Laas P. Pijnacker, [3]Leo W. Beukeboom, [4]Bas J. Zwaan

[1]Leiden University, Institute for Biology, Section of Animal Ecology, P.O. Box 9516, 2300 RA Leiden, The Netherlands

[2]University of Groningen, Groningen Biomolecular Sciences and Biotechnology Institute, Department of Genetics, P.O. Box 14, 9750 AA Haren, The Netherlands

[3]University of Groningen, Biological Centre, Section of Evolutionary Genetics, P.O. Box 14, 9750 AA Haren, The Netherlands

[4]Leiden University, Institute for Biology, Section of Evolutionary Biology, P.O. Box 9516, 2300 RA Leiden, The Netherlands

Parthenogenesis is found in many insect species and can be caused by a number of cytological mechanisms. A special case of parthenogenesis is that induced by intracellular bacteria of the genus *Wolbachia*. Parthenogenesis inducing (PI) *Wolbachia* are found in Hymenoptera but also in many other arthropod groups In only a few cases the cytological mechanism of *Wolbachia* induced parthenogenesis has been clarified. Different mechanisms have been found in different host species. Here we report on the cytological mechanism of *Wolbachia* induced parthenogenesis in *Leptopilina clavipes*, a parasitoid of *Drosophila* larvae. Using DAPI staining and fluorescence microscopy we show that the mechanism of parthenogenesis in *Wolbachia* infected *L. clavipes* is gamete duplication by segregation failure of the chromosomes in the first mitotic anaphase. The same mechanism has earlier been described in *Trichogramma* sp. (Stouthamer & Kazmer, 1994), but contrasts with the mechanism recently found in *Muscidifurax uniraptor* (Gottlieb et al., 2002). Furthermore, the cytology of infected wasps is compared to that of uninfected *L. clavipes*.

2.10

EVOLUTION OF INCOMPATIBILITY TYPES IN CI *WOLBACHIA* IS STRUCTURALLY UNSTABLE UNDER THE MOD-RESC HYPOTHESIS

[1]**Martijn Egas**, [2]Filipa Vala

[1]*University of Amsterdam, Institute of Biodiversity and Ecosystem Dynamics, Kruislaan 320, Amsterdam, The Netherlands*

[2]*Department of Biology, University College London, Wolfson House, 4 Stephenson Way, London, United Kingdom*

Wolbachia bacteria are obligate endosymbionts that are vertically transmitted from mother to offspring. The most widespread effect of *Wolbachia* on host reproduction is cytoplasmic incompatibility (CI). Here, *Wolbachia*-infected males are reproductively incompatible with uninfected females, or with females infected with a different strain of these bacteria. Although the molecular details are still unknown, *Wolbachia* are assumed to have two characters - one for modifying the sperm chromosomes (the 'mod' character) and one for rescuing these sperm chromosomes in the egg (the 'resc' character). When considering evolution of incompatibility types, assuming that mod and resc are different traits of *Wolbachia*, we run into a problem: a mutation in the resc function (from modArescA to modArescB) is fatal, because a female with such a mutant will be incompatible with all resident males, whereas a mutation in the mod function (from modArescA to modBrescA) makes a female carrying it incompatible with males carrying the same *Wolbachia* mutant. Recently, a theory has been put forward that does allow for evolution of such incompatibility types. In this paper, we show that this theory is structurally unstable for one assumption: the fitness of the mutant is equal to the fitness of the resident type. On the one hand, if the mutant's fitness is lower than the resident's, it cannot invade. On the other hand, if the mutant's fitness is higher than the resident's, the mutant will replace the resident and subsequently go extinct itself, thereby rendering the population uninfected. Hence, we need to consider alternative explanations for the existence of variation in incompatibility types. In absence of information on the molecular mechanism behind CI, we propose an alternative mod-resc mechanism, where both functions are governed by a single trait, and discuss how all known CI effects to date can be explained using this single-trait mechanism.

2.11

COMPETITION AND CO-OPERATION BETWEEN INTRACELLULAR INSECT SYMBIONTS WITHIN A COMMON HOST

R. D. J. Butcher

Centre for Population Biology, Imperial College, Silwood Park, UK

Many insect species are exploited by multiple species of intracellular symbionts, at least some of which can impact heavily on their host biology. Although intracellular symbionts are taxonomically and biologically diverse, transmission mode is considered crucial to the diversity of interactions observed between symbionts and their hosts. However, vertically (VT) and horizontally transmitted (HT) symbionts are expected to have conflicting evolutionary interests with respect to their "use" of the host and parasite virulence, whilst symbionts with the same transmission mode may still interact within the same host. To date studies have focused primarily on host interactions with single symbionts, ignoring the importance of competition between different symbionts exploiting the same host species. Hosts interact with different sets of symbiont species at different points in space and time with potentially important consequences for both ecological and evolutionary dynamics of the host species. Here, we illustrate a range of co-operative and competitive interactions between intracellular symbionts in the *Brassica* associated lepidopteran species *Plutella xylostella*. In the Cameron Highlands, Malaysia, both species are infected by a diverse array of shared and unique symbionts but (co-) infection frequencies appear and *Spodoptera litura* non-randomly distributed suggesting a range of potential interactions. Of these, co-operation between two VT *Wolbachia* isolates, each with different altered host reproductive modes, not only maintains each infection but also drives double infections through the population. However, fixation is prevented by temperature reduced VT rates and by competition with microsporidia. Competition between different microsporidia is related to both transmission mode and host tissue utilisation, but although microsporidia infections largely exclude VT bacteria via reduced VT and/or death of the host, they appear responsible for occasional HT of *Wolbachia*, including across species. Symbiont infection profiles differ across local and broad geographical ranges, but the role of host migration upon symbiont population dynamics awaits evaluation.

2.12

CASTRATION OF INTERMEDIATE HOSTS BY ACANTHOCEPHALAN PARASITES : ADAPTIVE TRAIT OR BY-PRODUCT OF MANIPULATION?

Marie-Jeanne Perrot-Minnot, Cédrik Juillet, Maria Gaillard, Frank Cézilly

Université de Bourgogne, 6 Blvd Gabriel, 21000 Dijon, France

Acanthocephalan parasites can induce various phenotypic alterations in their intermediate hosts, such as changes in appearance, physiology or behaviour. In particular, acanthocephalans are known to cause total or partial castration in their female hosts, whereas their effect on male reproduction is less clear. Here, we document the effects of two different species of acanthocephalan parasites on the reproductive biology of two amphipod hosts, *Gammarus pulex* and *G. roeseli*. We first document the patterns of pairing between infected and uninfected hosts, and compare the effects of the parasites on female and male reproduction. We then present some results on the uptake of carotenoids by parasites, and discuss its potential relation to the observed patterns of castration. We discuss our results in relation to current views on host manipulation by parasites.

2.13

THE EVOLUTIONARY ORIGINS OF VERTICAL TRANSMISSION IN MICROSPORIDIAN PARASITES

Judith E Smith, Rebecca S Terry, Jolene Galbreath and Alison Dunn

School of Biology, University of Leeds, Leeds, LS2 9JT, UK

Microsporidian parasites frequently make use of vertical transmission (VT) during their complex life cycles, yet its importance has never been specifically investigated. We have previously described a microsporidian, *Nosema granulosis*, which appears to be exclusively vertically transmitted and feminises its crustacean host *G. duebeni.* We have initiated screening program to investigate the diversity and distribution of VT microsporidia and to test to what extent vertical transmission is associated with traits such as reduced virulence and host sex ratio distortion (SRD). We sampled fifteen species of crustacea, via PCR of gonadal tissue/eggs with microsporidia specific small subunit rDNA primers, and found that VT microsporidia were ubiquitous in these hosts. Eleven VT parasites were detected in the crustacean survey and these fell into diverse lineages of the phylum Microspora. Evidence of host sex ratio distortion has been found for three out of four of these parasites tested to date. The novel sequence data was used to reconstruct the parasite phylogeny. Mapping of VT and SRD traits show that these have multiple origins and lead us to propose, that vertical transmission may be an ancestral transmission route, and that it is associated with host sex ratio distortion. If our observations on VT microsporidia in the crustacea are borne out within other host phyla these parasites may come to rival the bacterial endosymbionts in their importance as sex ratio distorters. We are currently extending our VT screen to a wider range of hosts including snails, insects and fish.

Posters

2.14P

EXTENDED PHENOTYPES: HOST INDUCED BODY SIZE VARIATION IN A PARASITIC FLY (TACHINIDAE)

[1]Jonas Ahnesjo, [2]Anders Forsman, [3]Emilio Civantos

[1]School of Biosciences and Process Technology, Växjö University, SE 351 95 Växjö, Sweden

[2]School of Biosciences and Process Technology, Växjö University, SE 351 95 Växjö, Sweden

[3]Departamento Ecologia Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), Madrid, Spain

The ecological and evolutionary consequences of host-parasite interactions have attracted considerable attention among evolutionary biologists. We studied interactions between the colour polymorphic pygmy grasshopper *Tetrix undulata* (Orthoptera: Tetrigidae) and the endoparasitic fly *Leiophora innoxia* (Meigen)(Diptera: Tachinidae) to examine if the dynamics of the polymorphism in grasshoppers is likely to be influenced by selection imposed by parasites; and to test for host-induced variation in parasite phenotypes. Our results revealed that about 2 % and 30 % of adult grasshopper collected from the same natural population in two subsequent years were parasitized. Parasite prevalence was independent of both sex and colour morph of the host. Pupae were larger if the parasite had developed in a female than in a male host, possibly reflecting a physical constraint on larval growth imposed by host body size. Pupal size was associated also with host colour morph, with individuals that had developed in dark morphs being smaller at pupation compared to those that developed in paler morphs. Pupae that failed to eclose or produced abnormal imagines were smaller than those that developed normally. Pupal size was highly correlated with thorax length in adults. Pygmy grasshoppers belonging to darker morphs warm up more quickly when basking and prefer higher body temperatures, compared to paler morphs. The dependence of parasite body size on host colour morph thus may reflect plasticity of growth and development of the larvae in response to differential host body temperature.

2.15P

A MODEL OF FEMALE CHOICE IN *WOLBACHIA* INFECTED POPULATIONS: CAN PREFERENCE FOR UNINFECTED MALES EVOLVE?

Fleur de Crespigny, Nina Wedell, Roger Butlin

School of Biology, University of Leeds, Leeds LS2 9JT, UK

The spread of the intracellular parasite, *Wolbachia*, within a population where it causes cytoplasmic incompatibility (CI) may be influenced by a variety of factors including transmission fidelity, fecundity costs and the degree of CI. In addition, *Wolbachia* may influence the evolution of female mating strategies. We modelled the spread of *Wolbachia* and the evolution of an allele encoding female preference for males uninfected with CI inducing *Wolbachia* in a hypothetical arthropod system. The relative importance of various infection parameters and their influence on the dynamics of the *Wolbachia* infection were also assessed.

2.16P

OCCURRENCE OF GYNODIOECY IN WILD BEET (*BETA VULGARIS* SSP. *MARITIMA* L.): A GENEALOGICAL APPROACH USING CHLOROPLAST DNA

Stéphane Fénart, Pascal Touzet, Jean-François Arnaud, Joël Cuguen

Laboratoire de Génétique et Evolution des Populations Végétales, UMR-CNRS 8016, FR CNRS 1818, Université de Lille I, F-59655 Villeneuve d'Ascq cedex FRANCE

The wild beet (*Beta vulgaris* ssp. *maritima*) is a wind-pollinated and perennial plant distributed along the coasts of Mediterranean and Western Europe. This species presents a particular breeding system: gynodioecy, which involves the occurrence of both male sterile (female) and hermaphroditic plants within natural populations. In this species, gynodioecy is due to cytoplasmic male-sterility (CMS), defined as "maternally inherited deficiency in producing viable pollen". This sexual polymorphism involves a genomic conflict: mitochondrial genome encodes for male-sterilizing factors, while nuclear genome encodes for restorers of male fertility. In accessions from a large part of the distribution area, RFLP analysis of mitochondrial DNA (mtDNA) polymorphism revealed that four out of the twenty mtDNA haplotypes are associated with male sterility. The present study was aimed at analysing chloroplastic sequence diversity in order to test the hypothesis of a single origin for CMS in wild beet. On the basis of a strong linkage disequilibrium between mitochondrial and chloroplastic genomes, we considered that the genealogy of the chloroplastic haplotypes could faithfully reflect the mitochondrial haplotypes one. Therefore we analysed chloroplastic diversity of a representative sample of the different mitotypes (including several individuals for each major mitotype, one *B. v.* ssp. *adanensis*, one *B. macrocarpa* and one *B. patula*). Although direct sequencing of three chloroplastic DNA fragments (*trn*K, *trn*D-*trn*T and *trn*L-*trn*F) revealed low nucleotide variation at the intra-species level, statistical parsimony provided a robust genealogy of the different chloroplastic haplotypes. In this genealogy, the positions of the four CMS-associated haplotypes strongly suggest that male sterility in wild beet has occurred multiple times independently.

2.17P

HOW DO MALE-KILLING BACTERIA KILL MALES?

Joanna Bentley, Zoe Veneti, Gregory Hurst

Department of Biology, University College, London

Male killing bacteria can be very common within species, making them a potent selective force. They are also common amongst species, making these selective pressures widespread. But what aspects of host biology will they select upon? To answer this question, we must understand the interaction between pathogen and host at a mechanistic level. We here present data as to how one male-killing bacterium, *Spiroplasma poulsonii*, detects the sex of *Drosophila* embryos and subsequently kills male hosts.

2.18P

FUNGAL LIFESPAN MANIPULATED BY A MITOCHONDRIAL PLASMID

Marc F. P. M. Maas, Carole H. Sellem, [1]Annie Sainsard-Chanet, [1]Alfons J. M. Debets, [1]Rolf F. Hoekstra

[1]Laboratory of Genetics - Wageningen University, The Netherlands

[2]Centre de Génétique Moléculaire CNRS, Gif-sur-Yvette, France

Some linear mitochondrial plasmids are known to induce senescence in filamentous fungi. They seem to act by inserting into the mitochondrial DNA, destabilizing the mitochondrial genome. Although such plasmids may be associated with senescence by default, in the filamentous ascomycete *Podospora anserina,* some type of plasmid insertions seem to extend lifespan rather than shorten it. We show that the insertion of a plasmid from the pAL2-1 family into the putative promoter region of the mitochondrial genes ND2 and ND3, leads to the transcriptional inactivation of these genes and the malfunctioning of respiratory complex I, resulting in a striking stabilization of the mitochondrial genome and a more than ten-fold increase in life span at the cost of both male and female fertility.

2.19P

ECOLOGY AND EVOLUTION OF HOMING ENDONUCLEASE GENES IN FUNGI (GENUS *OPHIOSTOMA*)

[1]Vini Pereira, [1]Austin Burt, [2]Ken Buck, [3]Clive Brasier

[1]Imperial College London, Silwood Park campus, Buckhurst Rd, Ascot, Berkshire SL5 7PY, UK

[2]Imperial College London, South Kensington campus, Exhibition Rd, London SW7 2BB, UK

[3]Forest Research Station, Alice Holt Lodge, Farnham, Surrey GU10 4LH, UK

Homing Endonuclease Genes (HEGs) are genetic parasites that are inherited at a super-Mendelian rate, and are predicted to get fixed in an outcrossed population if they invade it. They are often associated with and confer mobility to group-I introns. HEGs have a very broad phylogenetic distribution that includes viruses, archaeabacteria, protists, fungi, and plant (and even animal) organelles. In order to explain the long term persistence of HEGs a cyclic model of recurrent invasions and extinctions has been proposed that requires horizontal transmission of the HEGs. This model was based on the distribution of HEGs across yeast species from different genera. Here I report the results of an intra-genus and intraspecific PCR survey of 50 isolates from 13 *Ophiostoma* species for a mitochondrial group-I intron in the large sub-unit rDNA (rnl) gene. DNA sequences were used to reconstruct the phylogeny of the group-I introns, and of their hosts. Polymorphism was found for: a) the presence/absence and functional state of the intron (HEG) across species; and b) the presence/absence of the intron within 3 species, which have (putatively) functional HEGs. All the introns contain HEGs and their phylogeny is incongruent with the host phylogeny, providing evidence for a history of horizontal transfers. This is consistent with the cyclic model for HEG evolution, which predicts that the introns are currently invading the polymorphic *Ophiostoma* species.

2.20P

A POSSIBLE INFLUENCE OF *WOLBACHIA* IN THE *CHORTHIPPUS PARALLELUS* HYBRID ZONE

[1]Mario Zabal-Aguirre, [1]Francisca Arroyo, [1]Carmen López-Fernández, [2]Roger K. Butlin, [1]José L. Bella

[1]*Departamento de Biología, Facultad de Ciencias, Universidad Autónoma de Madrid, E-28049 Madrid (Spain)*

[2]*School of Biology, University of Leeds, Leeds, LS2 9JT, UK*

Hybrid zones are regions where two taxa meet, mate and leave viable hybrid offspring. These are rare situations that allow the *in situ* study of genetic divergence and genetic barriers. Their biological relevance leads them to be considered “natural laboratories” or “windows on evolutionary processes” (see Hewitt, 1988; Harrison, 1993). *Chorthippus parallelus parallelus* and *Chorthippus parallelus erythropus* are two grasshopper subspecies whose distributions overlap in the Pyrenees, where they form a hybrid zone consisting of several contact zones where the orography and their ecological requirements permit. It originated in the last post-glacial expansion which, after allopatric differentiation, yielded a secondary contact between Iberian and other European populations arriving from the other refuges in the Italian Peninsula, the Balkans and the Caucasus. The morphological, physiological, behavioural and genetic differences between these two subspecies (and their natural and laboratory hybrids) have been thoroughly studied during the last 20 years, and represent a singular model in Evolutionary Biology. These studies reveal a complex picture, in which a number of causes contribute to the structure and dynamics of the hybrid zone. However, none of these causes by itself is sufficient to explain this, nor why F1 hybrids are such a good example of Haldane´s Rule. On the other hand, *Wolbachia* is an endosymbiotic bacterium, found in the cytoplasm of insects and other organisms. Several strains of its better-known representative, *Wolbachia pipientis*, have been described. These bacteria have the potential to disturb the reproduction of their hosts, rendering even certain crosses incompatible. These effects can be grouped into three categories: induction of parthenogenesis, male feminization or cytoplasmic incompatibility. The latter involves, for example, infected males being unable to leave descendants when they mate with uninfected females. This has been proposed as a possible speciation agent, since it gives rise to a reproductive barrier between infected and non-infected populations, operating in one direction only (i.e., not reciprocally) (Werren, 1997; Wade, 2001). A PCR survey with the appropriate primers reveals significant differences in the level of infection with *Wolbachia* in pure Pyrenean populations of *C. p. erythropus*, *C. p. parallelus* and their natural hybrids. These promising, preliminary, results serve to develop new hypotheses concerning the origin and maintenance of this hybrid zone, and suggest that previous data and conclusions may require reinterpretation.

Symposium 3

Genetics of species differences

Organisers: Juergen Gadau & Leo Beukeboom

Roger Stevens Lecture Theatre 20

09.50 – 10.20	**Rieseberg, L. H.** Integration of Populations and Differentiation of Species
10.20 – 11.00	**Coffee**
11.00 – 11.30	**Via, S.** The genetic mosaic of speciation
11.30 – 12.00	**Barton, N.** The plausibility of parapatric speciation
12.00 – 12.20	**Miyatake, T.** Pleiotropic effects of clock genes and allochronic reproductive isolation
12.20 – 12.40	**Domazet-Loso, T.** An evolutionary analysis of orphan genes in *Drosophila*
12.40 – 14.00	**Lunch**
14.00 – 14.20	**Bensch, S.** Extreme conflict among mitochondrial and nuclear loci for phylogenetic patterns in *Phylloscopus* warblers
14.20 – 14.40	**Greenberg, A J.** Precise allelic substitution as a tool to study speciation and adaptation in *Drosophila*
14.40 – 15.00	**Haerty W.** Sexual isolation between natural populations of *Drosophila melanogaster* from Brazzaville (Congo)
15.00 – 15. 20	**Lineham, M. E.** How polygenic are the traits responsible for sexual isolation in fruit flies?
15.20 – 16.00	**Tea**
16.00 – 16.20	**Shuker, D. M.** The genetic basis of male hybrid sterility in a grasshopper hybrid zone: quantitative genetic and molecular approaches
16.20 – 16.40	**Pietsch, C.** The genetic architecture of courtship and mating behaviour of *Nasonia*
16.40 – 17. 00	**Gadau, J.** The evolution of non-flying males in the genus *Nasonia*
17.00 – 17.20	**Peire-Morais, A.** Non-mendelian inheritance of courtship behaviour in *Nasonia vitripennis* (Hymenoptera: Pteromalidae)

Invited talks

3.1

INTEGRATION OF POPULATIONS AND DIFFERENTIATION OF SPECIES

Loren H. Rieseberg

Indiana University, Biology Department, Bloomington, IN 47405

The study of speciation is largely founded on two conceptual advances. The first was Darwin's proposal that species differences are caused by natural selection. The second was Ernst Mayr's formulation of the biological species concept, which emphasized the importance of gene flow for holding species together and barriers to gene flow for keeping them apart. However, both of these fundamental advances have been questioned in recent years. The primacy of divergent natural selection has been challenged by models of speciation emphasizing population bottlenecks and genetic drift, and the importance of gene flow has been disputed because levels of gene flow appear to be too low to keep conspecific populations from diverging. Here, I review evidence from recent genetic studies to evaluate these claims. With respect to selection, evidence from quantitative trait locus (QTL) studies indicates that the majority of QTLs effecting species differences have effects in the same direction. This pattern is most consistent with divergence through directional natural selection; neutral divergence would result in a high proportion of QTLs with antagonistic effects. Likewise, a review of the gene flow literature reveals that there is sufficient gene flow in essentially all plant and animal species to enable the efficient spread of strongly favorable alleles, the most likely agents of collective evolution. Moreover, estimates of s for major QTLs are sufficiently large to facilitate their spread across the range of a species. Thus, gene flow probably does hold species together, but its traditional role as a force that constrains differentiation has been over-emphasized relative to its creative role as a mechanism for the spread of advantageous mutations.

3.2

THE GENETIC MOSAIC OF SPECIATION

Sara Via

University of Maryland

Speciation may begin with differentiation at only a few key genes or chromosomal blocks involved in differential adaptation. This makes incipient species genetic mosaics of divergently selected and neutral genes. Markers tightly linked to these two classes of loci would be expected to yield differing pictures of both evolutionary relationships between diverging lineages and the dynamics of ongoing processes such as gene flow. To understand the genetics of speciation, it will be crucial to study the genetic mosaic in diverging taxa. I will discuss analyses of markers linked or unlinked to key QTL involved in habitat use in host-associated races of pea aphids to illustrate the importance of the genetic mosaic in understanding the processes of adaptation and speciation.

3.3

THE PLAUSIBILITY OF PARAPATRIC SPECIATION

Nick Barton

ICAPB University of Edinburgh

Allopatric speciation is inevitable, as separate populations accumulate different and incompatible combinations of genes. An examination of the several mechanisms by which allopatric populations can diverge shows that these mechanisms can also occur in parapatry within a broad, continuous habitat. In order for parapatric speciation to be completed, genetic differences that arise in different places must come together in a single strong barrier to gene flow; again, there are several plausible ways by which this can happen. Thus, parapatric speciation is at least as plausible as allopatric speciation. Similar arguments suggest that in situations where selection can cause a single population to split into incipient species, it is more likely that divergence would spread out from one particular location: thus, parapatric speciation also seems more likely than sympatric speciation. I will discuss what kind of evidence might distinguish between alternative geographic settings for the origin of new species.

Contributed talks

3.4

PLEIOTROPIC EFFECTS OF CLOCK GENES AND ALLOCHRONIC REPRODUCTIVE ISOLATION

T. Miyatake

Okayama University, Fac. Agric., Tsushima-naka 1-1-1, 700-8530 Okayama, Japan

Allochronic reproductive isolation between intra- or inter-specific populations may be caused by the difference in mating time in a day of some insects, in timing of egg spawning of sea organisms, or in flowering time of plants. The mechanism by which a clock gene pleiotropically controlling life history and behavioral time-related traits cause a reproductive isolation is explained using a model species. Clock genes that pleiotropically control circadian rhythm and the time of mating may cause allochronic reproductive isolation in a tephritid fly (*Bactrocera cucurbitae*). Melon flies mate once a day, at dusk. Flies with a shorter circadian period (ca 22 h of locomotor activity rhythm) mated 5 h earlier in the day than those with a longer circadian period (ca 30 h). Mate choice tests demonstrated significant pre-mating isolation between populations with short and long circadian periods. Pre-mating isolation did not occur when the mating time was synchronized between the two populations by photoperiodic controls, indicating that reproductive isolation is due to variations in the time of mating and not any unidentified ethological difference between the two populations. We cloned the per gene of the melon fly that is homologous to the *Drosophila per*. The relative level of *per* mRNA in the melon fly exhibited a robust daily fluctuation under LD conditions. The fluctuation of *per* expression under DD is closely correlated to the locomotor rhythm in *B. cucurbitae*. These results suggest that clock genes can cause reproductive isolation via the pleiotropic effect as a change of mating time. In this talk, recent worldwide advances in molecular works in relation to clock genes and pre-mating reproductive isolation are focused. I also discuss an allochronic speciation as an indirect consequence of adaptation to different environments or habitats in view of a pleiotropic effect of clock genes controlling time-related traits.

3.5

AN EVOLUTIONARY ANALYSIS OF ORPHAN GENES IN *DROSOPHILA*

Tomislav Domazet-Loso, Diethard Tautz

University in Cologne, Institute for Genetics, Weyertal 121, 50931 Cologne, Germany

Orphan genes are protein coding regions that have no recognizable homologue in distantly related species. A substantial fraction of coding regions in any genome sequenced so far consists of such orphan genes, but their evolutionary and functional significance is not understood. We present a re-analysis of the *Drosophila melanogaster* proteome that shows that there are still between 26 - 29% of all proteins without a signficant match with non-insect sequences and that these orphans are under-represented in genetic screens. To analyse the characteristics of orphan genes in *Drosophila* , we have used sequence comparisons between cDNAs retrieved from two *D. yakuba* libraries (embryo and adult) and their corresponding *D. melanogaster* orthologues. We find that the cDNA library from adults yields double as many orphan genes than the one from embryos, suggesting a higher constraint on the use of conserved genes in embryos. The orphan genes evolve on average more than three times faster than non-orphan genes, although the width of the evolutionary rate distribution is similar for both classes. In particular, some orphan genes show very low substitution rates which are comparable to otherwise highly conserved genes. We propose a general model for orphan gene evolution that takes these large rate differences into account and suggests that they are caused by episodic phases of fast and slow divergence. The general characteristics of orphan genes in *Drosophila* suggest that they may be involved in the evolution of adaptive traits and that slow evolving orphan genes may be particularly interesting candidate genes for identifying lineage specific adaptations.

3.6

EXTREME CONFLICT AMONG MITOCHONDRIAL AND NUCLEAR LOCI FOR PHYLOGENETIC PATTERNS IN *PHYLLOSCOPUS* WARBLERS

[1]**S. Bensch**, [2]D. Irwin, [2]J. Irwin, [3]L. Kvist, [1]S. Åkesson

[1]*Lund University, Ecology Building, 223 62 Lund, Sweden*

[2]*Center for Tropical Research, Institute of the Environment, 1609 Hershey Hall, University of California, Los Angeles, CA 90095, USA*

[3]*Department of Biology, FIN-90014 University of Oulu, Finland*

In animals, mitochondrial DNA has become the standard molecule used for reconstructing species phylogenies, obtaining indirect measures of effective population sizes, and detecting historical population bottlenecks. The importance placed on mtDNA is out of all proportion to its size, which is only 0.001% the size of the nuclear genome. That the mitochondria may not accurately reflect a species phylogeny and sometimes could be seriously biased is emphasised by the fact that it exhibits a different mutation rate, mode of inheritance and effective population size than the nuclear genes. Moreover, the theoretical distribution of coalescence times across loci is highly variable, making a multiple loci approach preferable. Here we demonstrate discordance in phylogenies and population parameter estimates among one mitochondrial and four nuclear genes in a group of *Phylloscopus* warblers. We suggest that the incongruent pattern found in the willow warbler *P. trochilus* results from either population fluctuations over the time period when diversity in mitochondrial and nuclear DNA was accumulating, or historical introgression of nuclear genes from a closely related taxon.

3.7

PRECISE ALLELIC SUBSTITUTION AS A TOOL TO STUDY SPECIATION AND ADAPTATION IN *DROSOPHILA*

[1]**Anthony J. Greenberg**, [2]Jennifer R. Moran, [1]Jerry A. Coyne, [1]Chung-I Wu

[1]*Dept. of Ecology and Evolution, University of Chicago, 1101 E 57th St, Chicago, IL 60637, USA*

[2]*Committee on Genetics, University of Chicago, 1101 E 57th St, Chicago, IL 60637, USA*

A large number of theoretical studies has revealed that isolation between species can arise through a variety of mechanisms. To decide which theoretical model applies in a particular case, it is often necessary to replace alleles of putative isolation genes from one species with alleles from another while keeping the rest of the genome constant. It has recently become possible in *Drosophila melanogaster*, and we are using this technique to shed light on the mechanism of behavioral isolation between Zimbabwe (Z) and Cosmopolitan (M) populations of the species. Females from Zimbabwe are unwilling to mate with Cosmopolitan males and this discrimination may represent an incipient stage of speciation. We targeted the *desat2* locus, which is responsible for a polymorphism in female cuticular hydrocarbon (CH) profiles. CH are mating pheromones in *Drosophila* and differences in CH profiles may contribute to reproductive isolation between species and races. The functional copy of *desat2* is prevalent in African and Caribbean populations. A small deletion 5' of *desat2* appears to inactivate the gene. The deletion allele has spread throughout the rest of the world. Sequence analysis indicates that this spread may have occurred under the influence of positive selection. All strongly discriminating Z lines carry the functional *desat2* gene, suggesting that it may be involved in behavioral isolation between the Z and M races. We have introduced the African *desat2* allele into a Cosmopolitan line on a transgene and by replacement at the endogenous locus. Analysis of the fitness consequences of this allelic substitution has shown that introduction of the African *desat2* allele affects resistance to various stresses. The effect of the African allele on behavioral isolation is also being tested. Our results raise the possibility that behavioral isolation between Z and M lines arose as a pleiotropic by-product of adaptation.

3.8

SEXUAL ISOLATION BETWEEN NATURAL POPULATIONS OF *DROSOPHILA MELANOGASTER* FROM BRAZZAVILLE (CONGO)

[1]Wilfried Haerty, [2]Jacques Rouault, [2]Jean-Marc Jallon, [1]Maïalène Lesbats, [1]**Pierre Capy**

[1]*Lab. Populations, Génétique et Evolution, CNRS, 91198 Gif/Yvette Cedex, France*

[2]*Lab. Neurobiologie de l'Apprentissage de la Mémoire et de la Communication, Bât 446, Université Paris-Sud, 91405 Orsay Cedex, France*

A significant homogamy is detected between two populations of *Drosophila melanogaster* from Brazzaville. One population is found in the outskirts of the city on manioc and fruits (Loua = L) and the other on beer residues in a brewery (Kronenbourg = K). Hybrids between the two populations are perfectly viable and no post-zygotic isolation is observed. They do not show higher mortality or sterility compared to the parental populations. Cuticular hydrocarbons differences found between the two populations could partly be at the origin of the pre-mating isolation. Evolution of population cages with 50% of each population shows that a deficit in heterozygous for a marker (*AdhF*) can be maintained during two years (average *Fis* = 0.5). All these observations are not the result of a sympatric isolation. From the analysis of microsatellite loci and other genes, we can conclude that the brewery population is likely from an European origin. However, hybrids between the introduced and native populations probably occurred since few African characteristics can be found in the K population. In conclusion, this pre-mating isolation seems to be the result of a long term divergence between allopatric populations followed by a secondary contact due to the introduction of an European population in tropical Africa.

3.9

HOW POLYGENIC ARE THE TRAITS RESPONSIBLE FOR SEXUAL ISOLATION IN FRUIT FLIES?

[1]**M. E. Lineham**, [2]J-M Jallon, [1]M. G. Ritchie

[1]*University of St Andrews, Environmental & Evolutionary Biology, Sir Harold Mitchell Building, St Andrews, KY16 9TH, UK*

[2]*Université Paris Sud XI, NAMC, CNRS, UMR 8620, Bât 446, 91405 Orsay, France*

There has long been debate as to whether traits involved in reproductive isolation are controlled by many genes spread throughout the genome each contributing a small amount, or whether there are few genes, or even a single gene, of large effect. It has been suggested that behavioural traits involved in pre-mating isolation are likely to be highly polygenic due to their complex nature. Other related traits which influence mating behaviour, such as olfactory signals, may however be candidates for single gene control due to the more straightforward metabolic pathways involved. Female fruit flies of species within the *Drosophila melanogaster* species sub-group possess cuticular hydrocarbons, which act as contact pheromones, capable of inducing male courtship. The major courtship signal produced by males is wing vibration, often termed courtship song. Both these traits have been repeatedly shown to be involved in species recognition and sexual isolation. Here we examine the genetic basis for the variation in sexually isolating traits between *Drosophila simulans* and *D. sechellia*. Using Recombinant Inbred (RI) lines characterized for the trait and the composite interval mapping function in QTL Cartographer, we will identify potential Quantitative Trait Loci (QTL). These are specific regions in the genome which are associated with the quantitative trait of interest. Given high enough resolution this approach could help us to identify the number and location of genes involved.

3.10

THE GENETIC BASIS OF MALE HYBRID STERILITY IN A *CHORTHIPPUS* GRASSHOPPER HYBRID ZONE: QUANTITATIVE GENETIC AND MOLECULAR APPROACHES

[1]**D. M. Shuker**, [2]T. M. King, [2]R. K. Butlin

[1]*ICAPB, University of Edinburgh, Ashworth Laboratories, King's Buildings, Edinburgh, EH9 3JT, UK*

[2]*School of Biology, University of Leeds, Leeds, LS2 9JT, UK*

Progress in understanding the processes and speed of speciation will be considerably helped by understanding the genetic basis of species differences, including finding genes that contribute directly to speciation. The *Chorthippus p. parallelus – C. p. erythropus* hybrid zone in the Pyrenees is ideally suited for such a research program. In the field, hybrids are fully fertile, yet crosses between pure *parallelus* and pure *erythropus* individuals yield sterile males with degenerate testes (an example of Haldane's rule, since males are the hemizygous sex). Hybrid male fertility in the field has therefore been rescued in some way, perhaps through the reconstruction of fit ancestral genotypes by recombination. By crossing hybrids from the field with individuals of the pure sub-species, a cline in male hybrid dysfunction can be generated. Here we present two complementary approaches taken to explore this cline, and the genetic basis of hybrid dysfunction in *C. parallelus*. The first is a quantitative genetic study of testes dysfunction, estimating genetic parameters from the cline, including the number of genes involved in hybrid dysfunction. The second is an ongoing molecular study examining differentially expressed genes in the two sub-species, and how they vary through the hybrid zone. The number of differentially expressed sequences and putative genetic identity of these sequences will be discussed, and the merits of the two approaches contrasted.

3.11

THE GENETIC ARCHITECTURE OF COURTSHIP AND MATING BEHAVIOUR OF *NASONIA* (HYMENOPTERA: PTEROMALIDAE)

[1]C. Pietsch, [2]K. B. Rütten, [3]J.van den Assem, [1]J. Gadau, [3]**L. W. Beukeboom**

[1]*Institut für Verhaltensphysiologie und Soziobiologie, Universität Würzburg, 97074 Würzburg, Germany*

[2]*Biopsytec Analytik GmbH, 53359 Rheinbach, Germany*

[3]*Evolutionary Genetics Group, Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 14, NL-9750 AA Haren, The Netherlands*

Our knowledge of the genetic changes that occur during early speciation is still very limited. Some studies have shown that differences between related species are due to one or few genes with large effects, whereas in other studies evidence was found for many genes with small effects. A problem with these studies is to distinguish between the genetics of speciation (causing reproductive isolation) and the genetics of species differences (causing different phenotypes). A system especially amenable to study the genetics of incipient species differences is the *Nasonia* sibling species complex. We quantified courtship behaviour of hybrid males of *N. vitripennis* and *N. longicornis*. Hybrids showed, as expected, intermediate courtship behaviour between the parental species. However, in both reciprocal crosses a significant bias towards the (grand)father species was evident in most components of courtship analysed. We mapped QTL for several components of the courtship behaviour using STS, RAPD, AFLP and microsatellite markers. Based on microdissections of individual chromosomes we constructed chromosome specific markers for all five chromosomes of *Nasonia vitripennis* and verified their chromosomal specificity through *in situ* hybridization and linkage analyses. This information will allow us in the future to isolate the genes underlying the behavioural QTL more rapidly. We will present the results of a QTL analysis of the male courtship behaviour of F2-hybrids from a cross between *N. vitripennis* and *N. longicornis*.

3.12

THE EVOLUTION OF NON-FLYING MALES IN THE GENUS *NASONIA*

[1]Jürgen Gadau, [2]Fritz-Olaf Lehmann, [2]Nicole Heymann

[1]Julius-Maximilian-University, Zoology II, Am Hubland, 97074 Würzburg, Germany

[2]University of Ulm,BioFuture Research Group, Albert-Einstein-Allee 11, 89081 Ulm, Germany

There are considerable differences in male wing size (from female sized to vestigial) between three species of the parasitic wasp genus *Nasonia* and it has been assumed that flight performance of *Nasonia* males thus differs among these species. To test flight ability we have flown tethered individuals of both sexes of all three *Nasonia* species in a virtual flight arena under visual closed-loop feedback conditions. We measured total flight force production, wing kinematics and metabolic rate. Preliminary results suggest that all females could fly. *N. giraulti* males exhibit long lasting active flight of up to 40 min. In comparison, *N. longicornis* males show reduced flight performance and endurance that seems to be consistent with their smaller wing size. *N. vitripennis* males in contrast may actively flap their tiny wings during courtship but they are unable to sustain active flight. We conducted a full genomic screen for QTL affecting wing size and the detection of epistatic interactions in two hybrid crosses (*N. vitripennis* X *N. longicornis* and *N. vitripennis* and *N. giraulti*). These quantitative trait locus (QTL) analyses of the interspecific wing size difference revealed QTL with major effects and epistatic interactions among loci affecting the trait. Screening for pairwise epistatic interactions between marker loci on different linkage groups revealed additional loci for wing length and 4 loci for normalized wing size that were not detected in the original QTL analysis. Smaller wings and the associated loss of flight in *N. vitripennis* might have evolved as a reaction to an increase in local male-male competition compared to the other species due to habitat change. *N. vitripennis* also uses fly pupae around carcasses instead of fly pupae in bird nests with a potential for higher population densities. Recent population genetic data suggests that *N. vitripennis* experiences significant competition between unrelated males.

3.13

NON-MENDELIAN INHERITANCE OF COURTSHIP BEHAVIOUR IN *NASONIA VITRIPENNIS* (HYMENOPTERA: PTEROMALIDAE).

Aitana Peire-Morais, Albert Kamping, Louis van de Zande, Leo W. Beukeboom

University of Groningen, Biological Centre, Kerklaan 30, 9751NN, Haren (Groningen), The Netherlands

The three sibling species from the *Nasonia* group (*N. vitripennis, N. longicornis, N. giraulti*) broadly show similar courtship behaviour patterns but with species specific variations. Previous studies on hybrids between *N. vitripennis* and *N.longicornis* have shown a tendency of hybrid male sibship to behave as the grandfather's species. It is of special interest to find out whether this phenomenon occurs also within species. Different behavioural lines within *N. vitripennis* have been crossed and the male sibship scored, in order to test for the presence of this grandfather effect within species.

Posters

3.14P

HOST GENOTYPE AFFECTS WITHIN-HOST COMPETITION BETWEEN RODENT MALARIA PARASITES

J. C. De Roode, S. Cheesman, R. Culleton, R. Carter, A. F. Read

INSTITUTE OF CELL, ANIMAL AND POPULATION BIOLOGY, UNIVERSITY OF EDINBURGH, KINGS BUILDINGS, WEST MAINS ROAD, EDINBURGH EH9 3JT, SCOTLAND, UK

As with other organisms, malaria parasites compete for limited amounts of food, mates and space. Different parasites infecting the same host, for example, face competition for limited numbers of red blood cells. Competition affects parasite growth rate, transmission, and virulence, and is thus important for parasite evolution. Theory predicts that virulent clones outgrow avirulent ones, leading to the evolution of higher virulence. We infected laboratory mice with a mixture of two *Plasmodium chabaudi* clones: one virulent, the other avirulent. Using quantitative real- time PCR, we indeed found that the virulent clone overgrew the avirulent clone. However, whereas in one mouse strain the avirulent clone disappeared below detectible levels, in another strain it was only suppressed, and returned to overgrow the virulent clone later on during the infection. We suggest these differences may be explained by different immune responses to the two parasite clones in different mouse strains. Host immune status therefore seems an important factor in within-host competition between parasite clones and the evolution of parasite virulence.

3.15P

GENETIC AND MORPHOLOGICAL ANALYSES OF HOST RACE FORMATION IN *TEPHRITIS BARDANAE* (DIPTERA: TEPHRITIDAE)

Thorsten Diegisser, Jes Johannesen, Alfred Seitz

University of Mainz, Saarstrasse 21, 55099 Mainz, Germany

Host races are populations which are partially reproductively isolated from other conspecific populations as a consequence of adaptation to a specific host. We present evidence for host race formation in a tephritid fly which seems to be in the early stages of divergence. *Tephritis bardanae* infests flower heads of two burdock hosts, *Arctium tomentosum* and *A. minus*. Observations suggest host-associated mating and behavioural differences at oviposition indicating host-race status. Previously, flies from each host plant were found to differ slightly in allozyme allele frequencies but these differences could as well be explained by geographic separation of host plants. In the present study we explicitly test whether genetic and morphological variance among *T. bardanae* are explained best by host-plant association or by geographic location, and if this pattern is stable over a ten-year period. Populations of *A. tomentosum* flies differed significantly from those of *A. minus* flies in (i) allozyme allele frequencies at the loci *Pep-A* and *Pgd*, (ii) mtDNA haplotype frequencies and (iii) wing size. In contrast, geographic location had no significant influence on the variance estimates. While it remains uncertain whether morphometric differentiation reflects genotypic variability or phenotypic plasticity, the allozyme and mtDNA differentiation provide strong evidence for host race formation in *Tephritis bardanae*. However, the levels of differentiation are relatively low indicating that the system is in an early stage of divergence. This might be due to a lack of time (i.e. the host shift occured recently) or due to relatively high gene flow preventing much differentiation at loci not experiencing selection.

3.16P

PHYLOGENY OF SOME BIVALVE SPECIES INFERRED FROM 16S rRNA SEQUENCES

M. Fernández-Moreno, A. González-Tizón, A. Martínez-Lage, J. Méndez

Department of Cellular and Molecular Biology. Faculty of Sciences. University of A Coruña. A Zapateira s/n. 15071 La Coruña. Spain

Partial sequences of the 16S rRNA gene were obtained for: *Geukensia demisa*, *Chlamys varia*, *Astarte borealis*, *Cerastoderma edule*, *Solen marginatus*, *Ensis arcuatus*, *Ensis siliqua* and *Venerupis rhomboideus*, and compared with other mollusc sequences published. Two fragments (~ 525 bp L-band; ~ 600 bp H-band) were observed after partial amplification of the 16S rRNA gene. These results are similar to those described in different vertebrate and invertebrate groups. Different individuals were screened for this gene fragment, and all showed only one band, with the exception of *E. siliqua* which revealed two bands. Each band was sequenced. H-band(s) showed insertions located between positions 244 and 355, while L-band(s) contained two small insertions between positions 21 and 56. High homology was observed between H and L bands. The distance matrix obtained from the alignment of all sequences and the transition/transvertion ratios showed that all sequences are close to the saturation zone (values close to one). The Maximum-parsimony tree was supported by a high bootstrap value. The topology showed four clusters: one containing all the *Chlamys* species, another having *Geukensia demisa*, all H-bands and one L-band, the third showing *Venerupis rhomboideus* and the last one grouping the other L-bands, *E. arcuatus*, *S. marginatus* and *A. borealis*.

3.17P

COMPARING MORPHOMETRIC, ALLOZYME AND MITOCHONDRIAL DNA DATA IN A SLUG SPECIES COMPLEX (GASTROPODA, PULMONATA, ARIONIDAE).

Sofie Geenen, Kurt Jordaens, Jan Pinceel, T. Backeljau

University of Antwerp, Evolutionary Biology Group, Groenenborgerlaan 171, B-2020 Antwerp, Belgium

Royal Belgian Institute of Natural Sciences, Vautierstraat 29, B-1000 Brussels, Belgium

The subgenus *Carinarion* comprises three hermaphroditic slug species, i.e. *Arion fasciatus*, *A. circumscriptus* and *A. silvaticus*. The identification of these species is based on colour differences and subtle differences in the genitalia. In Northwest Europe, the species status is further supported by species specific alleles at several allozyme loci. However, recently we showed that in some Polish, German and Austrian *Carinarion* populations outcrossing may occur, producing heterozygote genotypes of alleles that in Northwest Europe are supposed to be characteristic for different species. In this study, we combine morphometric, allozyme and mitochondrial 16S rRNA sequence data of 1100 animals out of 90 populations to investigate genetic variation in a larger part of the distribution of this species complex. All animals were dissected and their genitalia were measured with callipers. Different allozymes of the hepatopancreas were screened with polyacrylamide gel electrophoresis (PAGE) and Single Stranded Conformation Polymorphism (SSCP) was used to determine different haplotypes of a fragment of the mitochondrial 16S rRNA sequence. All different haplotypes were sequenced afterwards. We show that 1) there are no unambiguous morphometric or colour differences to separate the three species 2) outcrossing may not be infrequent in Central and Eastern Europe, 3) the species specific allozyme markers disappear in Central and Eastern Europe and 4) that *Carinarion* may consist of more than three evolutionary lineages which are not related to colour morphs or genotypes based on allozymes.

3.18P

IS THERE A PARENT OF ORIGIN EFFECT ON COURTSHIP INHERITANCE IN *NASONIA*?

M. W. Kleefsman, L. P. W. G. M. van de Zande, L. W. Beukeboom

Evolutionary genetics, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands

Speciation is an important topic in evolution, but little is known about its causes. *Nasonia*, a haplodiploid parasitic wasp of house fly pupae, is a suitable organism to study speciation. Different species of *Nasonia* are separated by *Wolbachia* bacteria that cause cytoplasmic incompatibility. By removing *Wolbachia*, it is possible to get viable and fertile hybrids from interspecific crosses. Due to the haplodiploid system, it takes two generations to obtain hybrid males (grandsons). Each *Nasonia* species has its own characteristic courtship behaviour. The courtship behaviour of hybrid males was expected to be intermediate to their grandparents, but turned out to be biased towards the grandfather species. This effect is called the grandfather effect and is probably due to genomic imprinting. To gain more knowledge about the genetics behind this effect, we studied the courtship behaviour of *N. longicornis* and *N. vitripennis* hybrids. We manipulated the degree of paternally and maternally contributed genes by using different ploidy mutants that produce haploid or diploid eggs or sperm. Results of the courtship behaviour of these hybrids will be presented with respect to the grandfather effect.

3.19P

NEW SPECIES-SPECIFIC MOLECULAR MARKERS IN RAZOR CLAMS USING ISSR´S.

Luis Mariñas, Andrés Martínez-Lage, Ana González-Tizón, Josefina Méndez

Dep. Biología Celular y Molecular, Universidade da Coruña, A Zapateira s/n 15071 – La Coruña, Spain

Ensis siliqua and *E. arcuatus* (Mollusca, Bivalvia) are two razor clam species with important populations in Galician coasts (NW of Spain). Their exploitation has a great economical importance in this geographical area. The morphological differentiation between them is difficult owed to they are very similar, which is consequence of their similar lifestyles. Very little is known about the genus *Ensis* at molecular level, and their differentiation using DNA-based tests was not possible up to date. An appropriate molecular approach to start these type of studies is an anonymous PCR-based technique. Inter Simple Sequence Repeats (ISSR) can be used as molecular markers to detect polymorphism and to study the SSR distribution and frequency. In this work, ISSR amplification was performed using 20 primers homologous to microsatellite repeats and containing additional selective but degenerated anchor nucleotides. In PCR reactions, twenty individuals of both sexes from two populations of each species were employed. Only 8 primers amplified multiple bands, while the rest of primers resulted in no amplification or even smear. A total number of 15 bands were excised from agarose gels, cloned and sequenced. Search against GenBank didn't find similarities with any previous existing nucleotide sequence. >From these bands, three resulted specie-specific molecular markers, two for *E. arcuatus* and one for *E. siliqua*. In the first case, a band of 350 bp, amplified using primer MM12, and another one of 600 bp obtained with primer MM13, appear only in *E. arcuatus*. In the second case the specific band for *E. siliqua* is a 600 pb resulted from the amplification with primer MM18.

3.20P

GENE FLOW IN A HOUSE MOUSE CHROMOSOMAL HYBRID ZONE

[1]T. Panithanarak, [1]H. C. Hauffe, [2]J. F. Dallas, [1]J. B. Searle

[1]*Department of Biology, University of York, PO Box 373, York YO10 5YW, UK*

[2]*School of Biological Sciences, University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, UK*

The West European house mouse (Mus musculus domesticus) is subdivided into many chromosomal races. In the alpine valley of Valtellina, Northern Italy, two chromosomal races were described as the Upper Valtellina (UV) with metacentrics 2.8 and 10.12 and the Poschiavo (POS) which carries metacentric 8.12 and acrocentrics 2 and 10. These races produce unfit hybrids due to problems in chromosome pairing and segregation. The races occur together in Sommacologna and Sondalo, but otherwise occur in separate villages in the valley. To study gene flow between these races in Valtellina, we have scored 13 microsatellite loci using 179 mice from 16 villages. Seven of the microsatellite loci were mapped at centromeric regions of chromosomes 10 and 12 that differ between the races. Six other loci were located at the telomeres of chromosomes 10 and 12 and at the centromeres of other chromosomes shared between the two races. Considering separated UV and POS populations within the valley, allelic differences between the races were found at five centromeric loci of chromosomes 10 and 12 but at none of the other loci. This distinction was not found in Sommacologna and Sondalo where the UV and POS populations occur in sympatry. These results provide evidence for reduced gene flow at the centromeric regions of race-specific chromosomes in situations where there is not intense interbreeding.

3.21P

ADJUSTING THE FOCUS IN GRAPEVINE VARIATION

[1]Marzia Salmaso, [1]Cinzia Segala, [1]Claudio Moser, [1]Serena Varotto,
[1]Riccardo Velasco

[1]*Istituto Agrario San Michele all'Adige, via Mach San Michele a/A (TN), Italy*

[2]*University of Padova, Department of environmental agronomy and crop production Agripolis (PD), Italy*

Grapevine (*Vitis* sp.) is a perennial crop that shows an important genetic diversity among cultivars, wild species or hybrids. It has been a species recalcitrant to classical genetic analysis for long time. Nowadays, genomics offers the possibility to overcome traditional scepticism on breeding of perennial plants supplying powerful techniques to marker assisted selection. We are currently scavenging the grape genome by an ESTs-SNPs Approach. approx 4500 sequences have been produced from cDNA-library of Regent (a newly –bred multiply fungus- resistant cultivar of *Vitis vinifera*) and Pinot noir (high quality *Vitis vinifera* cultivar) and classified based on their sequence homology by BLAST analysis. To date 72 SNPs have been developed from the first two hundreds sequences (ESTs) analysed, selected from four sub-groups: 1) pathogen-related, 2) anthocyanin metabolism, 3) sugar metabolism and 4) cell signalling, based on agronomical interesting traits 30 *Vitis vinifera* cultivars, cultivated and wild type, chosen to represent most of the genetic diversity in V. vinifera, an interspecific hybrid and a different specie of *Vitis* have been used to evaluate the degree of polymorphism in grapevine. Frequency and distribution of DNA polymorphisms at these genes is under investigation. Furthermore, a population derived from a cross between the hybrid and *Vitis vinifera*, cv Teroldego, segregating for resistance to pathogens, berry colour and other quality traits, is currently used to map SSCPs identified from gene sequences. This study will contribute to elucidate the evolutionary forces that shape patterns of variability in Grapevine.

3.22P

ROBERTSONIAN METACENTRIC CHROMOSOMES OF THE MOUSE TEND TO COSEGREGATE IN THE FIRST MEIOTIC DIVISION OF MULTIPLE HETEROZYGOUS MALES AS REVEALED BY FISH ANALYSIS OF SPERMATOCYTE II METAPHASES

[1]M. Scascitelli, [2]F. Pacchierotti, [1]M. Rizzoni, [1]B.Gustavino, [3]F.Spirito

[1]*Department of Biology, University of Rome, Tor Vergata, via della Ricerca Scientifica snc, 00133 Rome, Italy*

[2]*Section of Toxicology and Biomedical Sciences, ENEA CR Casaccia, via Anguillarese 301, 00060 Rome, Italy*

[3]*Department of Genetics and Molecular Biology, C. Darwin, University of Rome, la Sapienza, Piazzale Aldo Moro 5, 00185, Rome, Italy*

Different approaches (karyotypic analysis of F2 specimens and of second meiotic divisions of F1 specimens) and contrasting results (random segregation or cosegregation of isomorphic chromosomes) have been described up to now in current literature about the segregation pattern of Robertsonian metacentric chromosomes of multiple heterozygous mice. In the present study, we reported data on the FISH (Fluorescent In Situ Hybridisation) analysis with telomeric probes of spermatocyte II metaphases of laboratory mice heterozygous for 2, 3 or 4 Robertsonian metacentrics with an all-telocentric background. The use of telomeric probes allowed to distinguish metacentric chromosomes from pairs of acrocentric ones, with their centromeric regions close to each other. Data showed that isomorphic chromosomes tend to cosegregate (metacentric with metacentrics, acrocentrics with acrocentrics) at an extent which depends on the karyotype of the specimens. The values found of cosegregation have a moderate effect on the efficiency of underdominant chromosomal rearrangements as reproductive isolation factors.

3.23P

NONDISJUNCTION RATES IN MEIOSIS I OF HOUSE MICE (*MUS MUSCULUS DOMESTICUS*) HETEROZYGOUS FOR DIFFERENT NUMBERS OF RB METACENTRIC CHROMOSOMES

[1]M. Scascitelli, [2]F. Pacchierotti, [3]M. Rizzoni, [1]B. Gustavino, [3]F. Spirito

[1]*Department of Biology, University of Rome, Tor Vergata, via della Ricerca Scientifica snc, 00133 Rome, Italy*

[2]*Section of Toxicology and Biomedical Sciences, ENEA CR Casaccia, via Anguillarese 301, 00060 Rome, Italy*

[3]*Department of Genetics and Molecular Biology, C. Darwin, University of Rome, la Sapienza, Piazzale Aldo Moro 5, 00185, Rome, Italy*

Dual-colour FISH (fluorescence *in situ* hybridisation) was employed to estimate anaphase I nondisjunction rate of specific chromosome arms involved in Robertsonian centric fusions, in the house mouse (*Mus musculus domesticus*). We investigated the variation of such a NDJ rate between laboratory mice heterozygous for one, two, three or four Robertsonian metacentric chromosomes. The simultaneous use of two different colour probes in the same spreads among the different karyotypes added information about the influence of a nondisjunctional event, occurring in a trivalent, on the probability of nondisjunction of another trivalent. The presence of these kinds of epistatic interactions could explain the stability of mouse chromosomal races with multiple Rb metacentric chromosomes and the efficiency of the latter as barrier to the gene flow (see Searle, 1993). The results suggested that NDJ rate is not influenced by the number of Rb heterozygous chromosomes in meiosis; we didn't find any clear trend for all but one Rb chromosome arms. A comparison of the NDJ rate variation for different arm chromosomes was achieved by using alternative sets of chromosomes painting probes; it seemed to be similar for the labelled chromosome arms. On the other hand, we studied the incidence of aneuploidy during the first meiosis in the female germ cell of individuals with multiple Rb heterozygous translocations; we found remarkable higher values compared to the male germ system and it let to suppose that the alteration of the female germ line could play an important role in the cladogenetic process.

3.24P

SYMPATRIC SIBLING SPECIES OF EAST AFRICAN CICHLID FISHES DIFFER IN SEX DETERMINING SYSTEMS

[1]A. M. Smith, [2]M. E Knight, [1]C. van Oosterhaut, [1]O. Seehausen

[1]*University of Hull, Dept of Biology, Cottingham Road, Hull England*

[2]*University of Southampton, Dept of Biology, Boldrewood, Bassett Crescent East, Southampton, England*

The cichlid fishes of the African Great Lakes are perhaps the best-known example of explosive speciation, though the mechanisms that underlie the diversity are poorly understood. Several of the lineages that have undergone explosive speciation possess extremely conspicuous colour polymorphisms. Previous work used empirical evidence to construct a novel model of sympatric speciation in East African cichlids by sex ratio selection. The model revealed multiple pathways for rapid and repeated sympatric speciation through the origin of novel colour morphs with strong assortative mating. Despite the lack of geographic isolation or ecological differentiation, the new species coexist with the ancestral species. We aimed to test one prediction of the models that states that sympatric sister species will differ in the heterogametic sex, plain coloured species having heterogametic females whereas orange or blotched species have heterogametic males. This was achieved by hybridising sympatric sister species with and without the blotch colour polymorphism and assessing the colour morphs and sex ratios of the offspring. The results support the model's predictions.

3.25P

GENETIC ARCHITECTURE OF *DROSOPHILA* SEX COMB TEETH NUMBER

[1]Haruki Tatsuta, [2]Toshiyuki Takano-Shimizu

[1]*National Institute for Environmental Studies, Tsukuba, Ibaraki, 305-8506, Japan*

[2]*National Institute of Genetics, Mishima, Shizuoka, 411-8540, Japan*

Male flies of subgenus *Sophophora* including *Drosophila melanogaster* have special bristles on the tarsus of fore legs, so-called sex comb, and the number of the bristles varies a lot between and within species. Since the sex comb is not usually observed in species belonging to subgenus *Drosophila*, which presumably diverged from the *Sophophora* 40Myr ago, it is likely that the sex comb has recently arisen in the *Sophophora* species. In this study, we made a F2 mapping population obtained from inbred lines, two chromosome-substitution strains, and two third-chromosome congenic strains to examine genetic basis for the development of sex comb in two strains of *D. simulans*. Using several QTL analysis methods, we found five QTL and estimated their genetic effects. Furthermore, a significant epistatic interaction was found between a QTL on the second chromosome and that on the third. The number of QTL identified and genetic effects were drastically changed, depending on the genetic background. Based on these results, we try to address the role of genetic background on the development of *Drosophila* sex comb and presume an order of expression of the candidates and their epistatic effects.

3.26P

HOW MANY FISH MAKE A BOTTLENECK?

Marnie H. Demandt

Department of Animal Ecology, Uppsala University, Norbyvägen 18 D, 752 36 Uppsala, Sweden

How many fish make a bottleneck? Bottlenecks occur when population experience severe, temporary reductions in size. The effect of bottlenecks on genetic variation was studied in populations of the roach (*Rutilus rutilus*) using sequence data of the mtDNA ATPase6 and 8 genes. In four Swedish lakes the natural fish populations had gone extinct due to acidification. Fish were reintroduced after the restoration of these lakes in the late 80s and in the beginning of the 90s. Now, 10-15 years after these well documented founder events fin samples were taken from the present population. The genetic variation of these populations was compared to four populations that had not experienced such a dramatic population contraction. The bottlenecked populations are expected to exhibit less genetic variation than the controls since the extant genetic variation is the legacy of recent population dynamics. Based on this study we tried to assess how small a reintroduction bottleneck has to be to cause a detectable effect in a population. Since the number of reintroduced specimen constituting the four founder populations was high we expect no effect of the population contraction at all if the founder population was large enough. In this study a new method using sequence data has been applied to test for bottlenecks. A comparison with more traditional methods (e.g. Rogers & Harpending, Tajima's D) for detecting bottlenecks is made.

Symposium 4

Natural hybridization and introgression: its role in evolution and conservation

Organisers: Thure Hauser, Michael L. Arnold & Michael M. Hansen

Roger Stevens Lecture Theatre 21

09.50 – 10.20	**Campbell, D. R.** Fitness of plant hybrids depends on the environment: long-term field studies with *Ipomopsis*
10.20 – 11.00	**Coffee**
11.00 – 11.30	**Bernatchez, L.** The integrated use of quantitative genetics, linkage mapping and functional genomics to investigate the basis of population divergence and reproductive isolation in a hybrid zone of the lake whitefish (Salmonidae)
11.30 – 12.00	**Bouck, A.** Mapping introgression and reproductive isolation in Louisiana Irises
12.00 – 12.20	**Babik, W.** A mosaic, bimodal hybrid zone between two species of newts (*T. vulgaris* x *T. montandoni*, Amphibia: Salamandridae)
12.20 – 12.40	**Hauser, T. P.** Frequency dependent male and female fitness of oilseed rape, weedy *B. rapa*, and their hybrids
12.40 – 14.00	**Lunch**
14.00 – 14.20	**Asami, T.** Interspecific asymmetry of cryptic isolation and hybrid vigor in hermaphroditic snails
14.20 – 14.40	**Nürnberger, B.** Barriers to gene flow produced by selection on quantitative traits in hybrid zones
14.40 – 15.00	**Christiansen, D. G.** How sexually reproducing hybrids remain hybrid: Microsatellite offspring genotyping in pure populations of the hybrid waterfrog *Rana esculenta*
15.00 – 15. 20	**Strehl, C-P.** Preventing Introgression in Ants by Shunting F1 Hybrids into the Sterile Caste
15.20 – 16.00	**Tea**
16.00 – 16.20	**Köhler, S. C.** Natural selection in tadpole cohorts in the *Bombina* hybrid zone
16.20 – 16.40	**Nolte, A.** An apparent hybrid species of *Cottus* displays novel traits that facilitate colonization of new ecological subregions within the Rhine drainage
16.40 – 17. 00	**Spaak, P** Predator induced hybrid superiority in *Daphnia*?
17.00 – 17.20	**Hauffe, H. C.** Local speciation and raciation in a chromosomal hybrid zone

Invited talks

4.1

FITNESS OF PLANT HYBRIDS DEPENDS ON THE ENVIRONMENT: LONG-TERM FIELD STUDIES WITH *IPOMOPSIS*

D. R. Campbell

University of California, Irvine, Department of Ecology & Evolutionary Biology, Irvine CA 92697, USA

One view of natural hybrid zones is that hybrids are unfit because of genomic incompatibilities but exist in a stable tension zone. An alternative view is that selection depends on the environment, for example favouring opposite traits in two parental habitats or favouring hybrids of particular genetic background in novel habitats. My colleagues and I have performed long-term experiments with two closely related plant species in the genus *Ipomopsis* to measure hybrid fitness and its dependence upon the environment. Such reciprocal transplants also provide insight into mechanisms of ecological speciation. In one experiment we planted F1 hybrid and parental seed into habitats of *I. aggregata*, *I. tenuituba*, and natural hybrids, and followed them for eight years through survival and production of seed to estimate lifetime fitness of these monocarpic plants. Hybrid fitness depended on both the direction of the cross and the environment. Lifetime fitness for hybrids of one cytoplasmic background was higher than for one or both parents in parts of the hybrid zone. In a second experiment we also planted F2 hybrids and backcrosses. After four years, survival of F2 plants remained indistinguishable from that of the parental species, yielding no evidence so far for hybrid breakdown. High reproductive success of the hybrids is possible because they suffer no detriment in pollen receipt by hummingbird pollinators, even though certain floral traits can experience disruptive selection in some years. Gas exchange and stable isotope studies revealed differences between the species and heterosis in water use efficiency, perhaps contributing to the success of hybrids in dry habitats. Together these results indicate that selection of hybrids is environment dependent. They also suggest that a complex mixture of divergent selection driven by pollinators and edaphic factors may have contributed to ecological speciation.

4.2

THE INTEGRATED USE OF QUANTITATIVE GENETICS, LINKAGE MAPPING AND FUNCTIONAL GENOMICS TO INVESTIGATE THE BASIS OF POPULATION DIVERGENCE AND REPRODUCTIVE ISOLATION IN A HYBRID ZONE OF THE LAKE WHITEFISH (SALMONIDAE).

L. Bernatchez

Biologie, Université Laval, Quebec, Canada

A large amount of ecological information now supports the role of divergent natural selection as the main cause of population divergence and reproductive isolation. Because the genetic architecture of phenotypic traits determines how selection operates on them, the refined understanding of the role of natural selection also requires detailed knowledge on the genetic basis of traits involved in adaptation and speciation. Thus far, researchers have been primarily interested by mechanisms of hybrid sterility and inviability, with less concern for genotype-environment interactions in natural conditions. Given the state of progress on the ecological mechanisms of population divergence, and that technology now exists to search whole genome for genotype-phenotype associations, it is time to investigate the genetic basis of phenotypic changes and reproductive isolation within the conceptual framework offered by the general theory of adaptive radiation. As for ecological mechanisms, the genetic basis of adaptation and reproductive isolation should be studied in the early steps of the process, as genetic differences that accumulate subsequently are less relevant. In this talk, I will present results of our ongoing efforts aiming to elucidate the genetic basis of adaptation and reproductive isolation by investigating a hybrid zone of lake whitefish populations from north-eastern North America. Our general approach is to synergically use three complementary fields of genetics: quantitative genetics, genome-QTL mapping, and functional genomics. Information derived from controlled crosses is then used to assess the extent of divergence and gene exchange among natural populations. Variation in patterns of "adaptive" genetic differentiation are then interpreted in the light of environmental heterogeneity in order to test the general hypothesis that levels of genetic exchanges in this natural hybrid zone is determined by the intensity of natural selection differentially acting, depending of specific environmental characteristics.

4.3

MAPPING INTROGRESSION AND REPRODUCTIVE ISOLATION IN LOUISIANA IRISES

[1]Amy Bouck, [1]Ed Kentner, [2]Sue Wessler, [1]**Mike Arnold**

[1]*Department of Genetics, Life Sciences Building, University of Georgia, Athens, Georgia 30602, USA*

[2]*Department of Plant Biology, Plant Sciences Building, University of Georgia, Athens, Georgia 30602, USA*

Studies of natural hybridization, introgression and hybrid speciation have often focused on barriers to crosses between divergent lineages. This approach and focus can be traced to Darwin and then to the Neo-Darwinian synthesis. More recently, this focus has been replaced by analyses of the evolutionary outcomes afforded by crosses between divergent lineages. Thus, a number of research groups now approach studies of natural hybridization and reproductive isolation from a different conceptual framework. This “new” framework can be illustrated by the following question: "How might the genetic architecture of both adaptive traits and reproductive barriers canalize the potentially creative evolutionary outcomes of hybridization between divergent lineages?" A portion of our research program has involved characterizing the genetic underpinnings of reproductive isolation between *Iris fulva* and *I. brevicaulis*. Linkage maps constructed using retrotransposon display markers, in backcross 1 populations, have identified genomic regions that demonstrate segregation distortion presumably due to heterospecific genetic interactions. From these results, we have been able to discern portions of the genomes of these two species that are resistant to introgression versus other regions that recombine, and even regions for which introgression seems to be selectively favored. We can combine these results with a QTL analysis of floral traits conferring prezygotic reproductive isolation between these species, and infer whether intrinsic genetic interactions would likely affect the dynamics of trait introgression and ultimately of the hybrid zone itself.

Contributed talks

4.4

A MOSAIC, BIMODAL HYBRID ZONE BETWEEN TWO SPECIES OF NEWTS (*T. VULGARIS* X *T. MONTANDONI*, AMPHIBIA: SALAMANDRIDAE)

W. Babik, J. M. Szymura, J. Rafinski

Jagiellonian University, Institute of Zoology, Ingardena 6, 30-060 Krakow, Poland

The smooth and Montandon's newts are sister species parapatrically distributed in lower elevations along the Carpathian Mts. They combine low overall genetic divergence with pronounced differences in male epigamic characters. We have studied in detail 33 populations from a 120 sq km area of sympatry in the Polish Carpathians, scoring the genetic variation at 7 allozyme and 1 microsatellite loci, mitochondrial DNA and male epigamic characters. Three populations from allopatric areas were sampled as a reference and 7 additional allopatric populations were studied to check for long distance introgression. Hybridization in the main study area is widespread, hybrids were found in all but one population, with mean frequency 23% and ranging up to 83%. Most of the hybrids were recombinants closer to either parental species, putative F1s were rare and the distribution of genotypes in many populations was bimodal. This indicates that hybridization is not common but hybrids are fertile and their fitness is not substantially reduced. Additionally, significant heterozygote deficit and linkage disequilibria found in populations where both parentals and/or hybrids were found point to strong assortative mating. We found a striking discordance between the pattern of nuclear loci and mtDNA introgression, the latter being much more broader. Although there is a weak association between the genetic composition of populations and their geographic position on a North-South axis, the microgeographic pattern is strongly mosaic. The genetic composition of populations and the breeding habitat characteristics (10 variables recorded) did not correlate. Stochastic processes resulting from frequent extinction/recolonization dynamics are the most plausible explanation of the pattern observed. The hybrid zone shows both bimodal population genetic structure caused by assortative mating and a mosaic spatial pattern and therefore seem to fulfil the requirements for the reinforcement of premating isolation to evolve.

4.5

FREQUENCY DEPENDENT MALE AND FEMALE FITNESS OF OILSEED RAPE, WEEDY *B. RAPA*, AND THEIR HYBRIDS

[1]**T. P. Hauser**, [2]C. Damgaard, [1]M. Pertl, [1]R. B. Jørgensen

[1]Plant Research Dept., Risø National Laboratory, P.O. Box 49, DK-4000 Roskilde, Denmark

[2]National Environmental Research Inst., Vejlsøvej 25, DK-8600 Silkeborg, Denmark

It is well known that the fitness of hybrids may depend on the environment, however, only few studies have addressed how the frequencies of parents and their hybrids affect each others fitness. To study this, we set up two experiments with oilseed rape (*Brassica napus*), *B. rapa*, and various hybrid classes, planted out in mixtures with different densities and frequencies, including pure plots. In both experiments the seeds were harvested and counted; in one experiment, the paternity of seeds produced by *B. rapa* were determined by a combination of molecular and morphological markers, and presence of a transgene. The number of seeds produced per plant depended strongly on the frequencies of plant types in the mixtures. Most excitingly, F1 hybrids produced much fewer seeds than *B. rapa* in the pure plots, but many more in the mixed plots. In the mixed plots, F1 plants even produced more seeds than oilseed rape at two out of three densities. Overall, *B. napus*, *B. rapa*, and backcrosses produced fewer seeds in mixtures where they each occurred at low frequencies, whereas F1 produced more seeds. Both vegetative and reproductive competition may cause these effects. In contrast to their seed production, F1 plants were not very successful as fathers. Among the seeds developed on *B. rapa* plants, the majority was always produced by *B. rapa* themselves. *B. napus* and F1 plants almost only sired seeds if they completely dominated the mixtures. Our results clearly show that the male and female fitness of *both* hybrids *and* their parents are strongly frequency dependent, and we guess that this may be the case for other species as well. Our results also show that even if hybrids may be doing well as mothers, they may at the same time be poor fathers.

4.6

INTERSPECIFIC ASYMMETRY OF CRYPTIC ISOLATION AND HYBRID VIGOR IN HERMAPHRODITIC SNAILS

[1]**Takahiro Asami**, [2]Keiichi Seki

[1]*Shinshu University, Matsumoto 390-8621, Japan*

[2]*Toho University, Funabashi 274-8510, Japan*

MtDNA and allozyme markers indicate introgressive hybridization between native and alien species of snails, *Bradybaena pellucida* (*BP*) and *B. similaris* (*BS*), respectively. Their assortative mating is incomplete even when conspecific mate choice is allowed. These hermaphrodites ought to perform reciprocal courtships and penial insertions simultaneously and symmetrically between mates for a successful copulation, between species as well as within species. Despite of such symmetric copulation achievement between species, *BS* produces no offspring while *BP* normally reproduces. This asymmetric reproductive isolation results from a cryptic (post-mating but pre-zygotic) mechanism: Within each species, a mating pair exchanges spermatophores at the end of copulation. *BS* gives a mate a spermatophore and ends copulation earlier than *BP*. Because of their difference in copulation duration, *BS* can give a spermatophore to *BP* but fails in receiving it from *BP*. Thus, in interspecific mating, *BS* can be only the father, whereas *BP* can only the mother. On the other hand, F1 and F2 hybrids produced by *BP* exhibit hybrid vigor in growth and fecundity. Thus, there is no detectable post-zygotic breakdown. Because of their asymmetric cryptic isolation, introgression of mtDNA has been expected to be one-way from *BP* to *BS*, in contrast with nuclear alleles. However, both mtDNA and allozyme alleles exhibit two-way introgression. The two-way mode of mtDNA can only be possible through F2 production by *BS* backcrossed to F1 hybrids. In these animal hermaphrodites with low vagility, asymmetric cryptic isolation by divergence of copulation duration has been playing a key role in recent introgressive hybridization with an introduced species.

4.7

BARRIERS TO GENE FLOW PRODUCED BY SELECTION ON QUANTITATIVE TRAITS IN HYBRID ZONES

B. Nürnberger

University of Munich, Karlstr. 23, 80333 München, Germany

Hybrid zones between ecologically divergent taxa often form at ecotones. Natural selection on those phenotypic traits that mediate differential adaptation should then play an important role in stabilising these hybrid zones. Moreover, they result in barriers to gene flow for neutral variants, such as diagnostic molecular markers. These barriers delay but do not ultimately prevent the homogenisation of unselected allele frequency differences. Multilocus models predict that the barrier effect depends on the distribution of the total selection across the genome and on the magnitude of the resulting linkage disequilibria. In contrast, clines in phenotypic traits have been analysed in a quantitative genetic framework, which predicts changes in the mean and the variance but does not lend itself to a full analysis of the expected strong linkage disequilibria. I present results from a simulation model in which the genetic basis of several phenotypic traits in a hybrid zone is explicitly specified and varied. The model predicts the resulting phenotypic clines, the interactions among traits that are differently strongly selected and the resulting net barrier effects on interspersed neutral loci. These results allow predictions about the long-term fate of hybrid zones in their approach to an ultimate migration-selection equilibrium.

4.8

HOW SEXUALLY REPRODUCING HYBRIDS REMAIN HYBRID: MICROSATELLITE OFFSPRING GENOTYPING IN PURE POPULATIONS OF THE HYBRID WATERFROG *RANA ESCULENTA*

Ditte Guldager Christiansen, Kaare Fog, Bo Vest Pedersen, Jacobus J. Boomsma

University of Copenhagen, Zoological Institute, Departments of Evolutionary Biology and Population Ecology, Universitetsparken 15, 2100 Copenhagen, Denmark

Unlike in plants, speciation by hybridization is very rare in animals, and almost all of the hybrid forms are limited to clonal or hybridogenetic reproduction (reproduction with one of the parental species). Pure populations of the waterfrog, *Rana esculenta*, constitute an exceptional case of a sexually and independently reproducing hybrid animal species. R. esculenta is a hybrid between *R. lessonae* and *R. ridibunda*, and in most of its range it reproduces hybridogenetically. However, pure populations, always comprising both diploid and triploid individuals (but no non-hybrids), have been reported from several countries around the Baltic Sea. Here I present one of the first genetic marker studies on how these hybrids reproduce. I collected eggs from copulating pairs in three Danish populations and determined the genotypes of both healthy and abnormally developing offspring. Many aneuploids (with fractioned chromosome sets), some non-hybrids, and a few tetraploids were found as embryos, but only diploids and triploids survived and develop into healthy-looking metamorphs. The results imply a serious disadvantage for these pure hybrid populations, as many zygotes are inviable due to errors in meiosis and incompatibility of gametes. Nevertheless, *R. esculenta* is abundant in large areas where the parental species do not occur. All offspring were genotyped by scoring diagnostic alleles for the respective genomes of the parental species at 5 microsatellite loci, and by quantifying the relative amounts of PCR-amplified DNA for each of 2 of the same loci. This completely new method for genotyping waterfrogs has proved to be both accurate and highly informative.

4.9

PREVENTING INTROGRESSION IN ANTS BY SHUNTING F1 HYBRIDS INTO THE STERILE CASTE

[1]**Christoph-P. Strehl**, [1]Jürgen Gadau, [2]Kirk E. Anderson, [2]Robert A. Johnson,
[2]Jennifer H. Fewell

[1]*Theodor-Boveri-Institute, Department of Behavioral Physiology and Sociobiology (ZooII), Biocenter, University of Wuerzburg, D-97074 Würzburg, Germany*

[2]*Department of Biology, Arizona State University, Tempe, Arizona 85287, USA*

The harvester ants *Pogonomyrmex barbatus* and *P. rugosus* (Hymenoptera; Formicidae) show a broad zone of overlap where hybridization is documented by both behavioral observations at mating leks and molecular markers (RAPD, allozymes, microsatellites, mtDNA). Three independent studies of this hybrid zone at a site in southeastern Arizona, USA, found that all queens and sexuals were homozygous for species-specific markers whereas workers from the same colonies were exclusively heterozygous for the same markers (Volny et al. 2002, PNAS 99: 6108-6111; Julian et al. 2002, PNAS 99: 8157-8160; Cahan et al. 2002, Proc. R. Soc. Lond. B 269: 1871-1877), suggesting a system of genetic caste determination.

This system bears a clear fitness cost to founding colonies in species with claustral and haplometrotic colony founding like *Pogonomyrmex* because it can result in producing sexuals at a time in the colony cycle when these individuals are detrimental to colony survival. In fact, founding colonies were so far not observed producing sexuals. We tested whether absence of sexuals early in the colony cycle is 1) due to selective infanticide of homozygous brood or 2) ontogenetically driven due to differential survival of reproductive and non-reproductive brood. We reared founding colonies from sympatric and allopatric populations and determined the genotypes of queens, brood and adult workers. Our first results showed that homozygous individuals occur among the brood in hybrid populations, but they are lacking among the first adult workers. Therefore, we conclude that homozygous individuals are physically eliminated by the workers, the queen, or both.

The ability to shunt non-conspecific offspring into sterile castes offers eusocial species a unique mechanism for countering the negative fitness consequences of hybridization. Eusociality may thus paradoxically contribute to hybrid colony success but in turn limit the extent of hybridization beyond the F1 generation.

4.10

NATURAL SELECTION IN TADPOLE COHORTS IN THE *BOMBINA* HYBRID ZONE

[1]**S. C. Köhler**, [2]T. H. Vines, [3]T. R. Sands, [1]W. Gabriel, [1]B. Nürnberger

[1]*University of Munich, Karlstr. 23, 80333 München, Germany*

[2]*University of British Columbia, 6270 University Boulevard, Vancouver V6T 1Z4, Canada*

[3]*University of Edinburgh, King's Buildings, Edinburgh EH9 3JT, Scotland*

Adaptation to reproduction in ponds and puddles, respectively, has led to marked phenotypic divergence between the fire-bellied toads *Bombina bombina* and *B. variegata*. Yet, in zones of parapatric overlap, the two taxa hybridise freely, and one finds a wide spectrum of recombinants. Natural selection must therefore be acting to keep the two taxa from merging into one. Hybrid tadpoles in particular may be confronted with habitats to which they are not adapted. We took small samples from naturally laid egg batches, and, towards the end of the larval period, we collected the remaining tadpoles in 14 sites in the hybrid zone near Cluj, Romania. Measurements of tadpole size and shape were also taken. All animals were genotyped at five unlinked marker loci, which allow the assignment of tadpoles to egg sibships. We present family-specific growth rates and survivorships as functions of genotype and habitat.

4.11

AN APPARENT HYBRID SPECIES OF *COTTUS* DISPLAYS NOVEL TRAITS THAT FACILITATE COLONIZATION OF NEW ECOLOGICAL SUBREGIONS WITHIN THE RHINE DRAINAGE

[1]**A. Nolte**, [2]J. Freyhof, [1]D. Tautz

[1]*University of Cologne, Institute for Genetics, Weyertal 121, 50931 Cologne, Germany*

[2]*Institute for Freshwater Ecology and Inland Fisheries, Dept. 4, 12587 Berlin, Germany*

Phylogeographic studies of *Cottus gobio* using mitochondrial D-loop sequences have revealed deeply split clades with specific patterns of distribution across Europe. Most mitochondrial lineages are confined to separate drainage systems indicating that there cannot have been much mixture of genotypes in the past few million years. However, within the lower River Rhine system we found a mixture of divergent haplotype lineages, which may be due to recent secondary contact of previously separated lineages. In order to understand the nature of the possible hybrid genotypes, we have studied the population structure within the lower Rhine system combining evidence from genetics, morphology and distribution. It is possible to distinguish two divergent ecomorphotypes of *Cottus* with a high degree of genetic differentiation. One type corresponds to the autochtonous haplotype lineage while the other one carries additional immigrant haplotypes in its gene pool. Data on the ecology and population dynamics indicate a strong autecological differentiation of the types. The autochtonous lineage corresponds in ecology to what is thought to be typical for *C. gobio* . The hybrid lineage displays a life history, which is not found in other populations within the Rhine. In contrast to the autochtonous types, it lives in the summer-warm reaches of bigger rivers (potamal) and spreads along the main course of the Rhine. We will present the results of an extended survey based on nuclear markers which is designed to clarify whether the new type is indeed a hybrid between nuclear and mitochondrial lineages and which should allow to infer the time of the hybridization event.

4.12

PREDATOR INDUCED HYBRID SUPERIORITY IN *DAPHNIA*?

[1]**Piet Spaak**, [2]Maarten Boersma

[1]EAWAG, Dept. Limnology, Überlandstrasse 133, 8600 Dübendorf, Switzerland

[2]Alfred-Wegener-Institut für Polar und Meeresforschung, Biologische Anstalt Helgoland, Postfach 180, 27483 Helgoland, Germany

Different *Daphnia* (waterflea) species and their hybrids coexist in many lakes. We studied the potential influence of predatory fish on the maintenance of these species complexes using 20 *Daphnia* clones, belonging to 5 hybrid and parental taxa of the *Daphnia galeata-cucullata-hyalina* complex originating from the Plußsee (Northern Germany). With these clones a life-history experiment was conducted in water with and without fish kairomones. We found that fish kairomones reduces size at birth and size at maturity significantly. For size at maturity larger taxa showed a significantly stronger reaction to fish kairomones than the smaller taxa. To test how these life-history differences effect the competitive abilities of hybrids and parental species we did a competition experiment under semi-natural conditions. The experiment was done with the same 20 clones, which could be distinguished with allozyme electrophoresis, in two large-scale indoor containers, the plankton towers in Plön. We varied the food level, the presence of fish and kairomones. Using allozyme electrophoresis we observed clonal variation for Diel Vertical Migration. Without fish, two clones belonging to the largest taxa (*D. galeata* and *D. galeata x hyalina*) were numerically dominant. However, when fish was present relative densities of smaller *D. cucullata x galeata* clones were highest. The results of this experiment with respect to overall taxon success were in concordance with the life history study, but we could not predict the individual clonal success from the life-history experiment only. We conclude that both life history and behavioural data are needed to understand the success of individual clones in a predatory environment. Furthermore, our study shows that fish predation might be an important factor facilitating the co-occurrence of *Daphnia* parental taxa with their hybrids.

4.13

LOCAL SPECIATION AND RACIATION IN A CHROMOSOMAL HYBRID ZONE

[1,2]**H. C. Hauffe**, [1]T. Panithanarak, [1]J. Piálek, [3]J. F. Dallas, [1]J. B. Searle

[1]*Dept. of Biology, University of York, York YO10 5YW, U.K.*

[2]*Present address: Centre for Alpine Ecology, 38040 Viote del, Monte Bondone, Trento, Italy*

[3]*Dept. of Zoology, University of Aberdeen, Tillydrone Ave., Aberdeen AB24 2TZ, U.K.*

It is well-recognized that hybrid zones may provide insight into the process of speciation. In recent years, the house mouse (*Mus musculus domesticus*) has been extensively studied in this regard as several chromosomal hybrid zones of this species exist in Europe and North Africa. These hybrid zones form when two 'races', defined as populations homozygous for different centric (Robertsonian: Rb) fusions, come into contact. In 1989, we identified such a hybrid zone in Upper Valtellina, Province of Sondrio, Italy, which is characterized by 32 different karyotypes, including five Rb races (distributed in patches) and 27 hybrid types. At that time we hypothesized 1) that the differences in chromosome compliment between races should result in selection against hybrids and speciation by reinforcement, but that such speciation may require specific circumstances (e.g. small population size, low migration rates, etc.); 2) that hybridization could result in the creation of new races in a process we termed 'zonal raciation'. For hypothesis (1), we proceeded to quantify a number of parameters using a wide variety of field and laboratory techniques which could be used in computer simulations to predict the probability of speciation: population size, migration rate, selection against hybrids and genetic distance. In addition, behavioural experiments were used to test for reinforcement in the field and molecular studies aimed to identify part of the genome where gene exchange is suppressed. For hypothesis (2) microsatellite markers were used to identify the origin of the relevant chromosomes in the 'new', apparently hybrid race. We have strong evidence that reinforcement and zonal raciation may be occurring/has occurred in different areas of this hybrid zone. This presentation summarizes our results and conclusions.

Posters

4.14P

INTRASPECIFIC HYBRIDIZATION, DEVELOPMENTAL STABILITY AND FITNESS IN *DROSOPHILA MERCATORUM*

[1]Ditte Holm Andersen, [2]Cino Pertoldi, [1]Valerio Scali, [3]Volker Loeschcke

[1]Universitá di Bologna, Via Selmi 3, I-40126 Bologna, Italy

[2]National Environmental Resaerch Institute, Kalø, Grenåvej 14, DK-8410 Rønde, Denmark

[3]University of Aarhus, Ny Munkegade, Buid. 540, DK-8000 Aarhus, Denmark

One of the possible effects of intraspecific hybridization is outbreeding depression, due to a breakdown of coadapted gene complexes, which can lead to reduced fitness and decreased developmental stability in hybrids. Alternatively, increased fitness and increased developmental stability in hybrids (hybrid vigour) may be a result of hybridization, probably due to increased heterozygousity. Developmental stability is assumed to be correlated with fitness and is commonly measured as fluctuating asymmetry or phenotypic variance. *Drosophila mercatorum* is capable of reproducing sexually, but also parthenogenetically in the laboratory. When selecting for parthenogenesis, the flies become homozygous in one generation; strong selection, is acting on the genome for coadaptation among genes. Intraspecific hybridisation is therefore expected to have an impact when coadaptation is disrupted. Intraspecific hybridization between a parthenogenetic and a sexually reproducing strain of *Drosophila mercatorum* resulted in significant changes in fecundity as well as fluctuating asymmetry and phenotypic variance for the number of sternopleural bristles and in the length of two wing traits over three generations after hybridisation. We found a `hybrid vigour′ effect in F1 females with an increase in fecundity relative to their parental populations. The F2 and the F3 females showed increased fluctuating asymmetry in several traits and reduced fecundity compared with the F1 females, probably due to a breakdown in coadapted gene complexes. The males followed the same pattern of fluctuating asymmetry for bristles but there was no increase in wing fluctuating asymmetry in the F2 and F3 generations. We found an increase in phenotypic variance in the F1 generation for both sexes and all traits, which could be due to increased genetic variance after hybridisation. The phenotypic variance increased further in the generations F2 and F3 for bristle number. For the wings, phenotypic variance generally decreased in generations F2 and F3 when compared with F1, which we attribute to canalization and selection on the wings.

4.15P

EVOLUTIVE HISTORY OF THE *PHOXINUS* COMPLEX IN NORTH AMERICA

M.-C. Binet, B. Angers

University of Montreal, succ Centre Ville, 6128,Montreal, Québec, Canada

Phoxinus eos and *P. neogaeus* are 2 cyprinids species able to hybridize. These hybrids can not backcrossed with pure species but reproduce asexually by gynogenesis. Occasionally, the male's genome is incorporated and triploid individuals are obtained. Sometimes, the *P. neogaeus*'s genome can be eliminated, giving birth to diploid *eos* with *P. neogaeus* mitochondrial DNA. All of the above occurrences can be observed within a given lake and it is not possible to morphologically identify these individuals. The molecular signature of these hybridization events can be detected with the help of molecular markers. In this project, mitochondrial DNA and microsatellites markers were developed and used conjointly to identify each of the members of the *Phoxinus* complex. Preliminary tests revealed a high degree of polymorphism that allow us to bring out the recent history of the populations of this complex.

4.16P

INTROGRESSIVE HYBRIDIZATION IN IBERIAN *BARBUS* SPP. (TELEOSTEI, CYPRINIDAE) IN THE GUADIANA RIVER BASIN AS REVEALED BY MORPHOLOGICAL AND MOLECULAR MARKERS

[1]Hugo F. Gante, [2]Thomas E. Dowling, [3]M. Judite Alves

[1]*Centro de Biologia Ambiental and Museu Nacional de História Nacional da Universidade de Lisboa, Rua da Escola Politécnica 58, 1269-102 Lisbon, Portugal*

[2]*Department of Biology, Arizona State University, Tempe, Arizona 85287-1501, U.S.A.*

[3]*Centro de Biologia Ambiental and Museu Nacional de História Nacional da Universidade de Lisboa, Rua da Escola Politécnica 58, 1269-102 Lisbon, Portugal*

Hybridization among the Iberian endemic *Barbus* spp. inhabiting the Guadiana River Basin was assessed using morphological and molecular markers. Multivariate analyses of meristic characters and relative warps of landmark characters showed a high number of intermediate phenotypes, which have historically been interpreted as phenotypic plasticity. SSCP analyses of a fragment from the mitochondrial cytochrome *b* gene showed a non-concordant pattern compared to morphology, raising the hypothesis of introgression. Introgression of mtDNA is interpreted relative to local scenarios of species abundances and distribution area.

4.17P

RE-EVALUATION OF GOLDSCHMIDT?S CROSSES IN THE GYPSY MOTH, *LYMANTRIA DISPAR*, IN RELATION TO HYBRIDIZATIONS BETWEEN SUBSPECIES

[1]Y. Higashiura, [2]M. Ishihara, [1]N. Ono, [1]H.Yamaguchi, [3]P. W. Schaefer

[1]*Tokyo Univ. of Pharmacy and Life Science, Hachioji, Tokyo 192-0392, Japan.*

[2]*Hyogo College of Medicine, Nishinomiya, Hyogo 663-8501, Japan*

[3]*USDA, Beneficial Insects Introduction Research Laboratory, 501 S-Chapel Street, Newark, DE 19713-3814, USA*

Richard Goldschmidt mated different geographical varieties of gypsy moth, *Lymantria dispar*, and proposed his theory of sex determination. That mating included hybridizations between subspecies, and resulted in abnormal sex conditions. We studied mitochondrial DNA variation in the gypsy moth in Japan. Using these data of haplotype distribution, we re-evaluate the Goldschmidt crosses in relation to hybridizations between subspecies.

4.18P

NUCLEAR AND MITOCHONDRIAL GENE FLOW IN A BOMBINA HYBRID ZONE

Sebastian Hofman, Jacek M Szymura

Jagiellonian University, Institute of Zoology, Ingardena 6, 30-060 Krakow, Poland

We analyzed patterns of nuclear and mitochondrial DNA variation in two transects across a hybrid zone between the fire-bellied toads (*Bombina bombina* and *B. variegata*) in Poland: near Kraków and Przemyœl, using 6 diagnostic allozyme loci and RFLP haplotypes of an amplified mtDNA fragment. Clinal variation of the markers appears highly correlated, but suprisingly, mtDNA introgression was significantly reduced relative to allozymes. MtDNA cline width (w=3.42 km) was nearly half of the allozyme cline (w=6.05 km). Moreover, it was significantly shifted towards the bombina side of the zone by 0.96 km. Two factors, dispersal and selection, may be involved in producing dissimilar variation patterns at nuclear loci and mtDNA haplotypes. An unequal dispersal rate between the sexes can account for the narrowing of the mtDNA cline, if females move over shorter distances than males. On the other hand, a different dispersal rate between the species could explain directional introgression of mtDNA haplotypes. Higher dispersal of females with the variegata haplotype would lead to the mtDNA cline shifting towards the bombina side. Differences in cline widths may also indicate selection. Narrowing of the mtDNA cline suggests that DNA regions involved in coadptation between the nuclear and mitochondrial genes are under relatively strong selection. This is expected given the high divergence between the two *Bombina* species at the molecular level. The shift of the mtDNA cline to the bombina side would imply different selection on each sex. This asymmetry may suggests that in *bombina*-like habitats hybrid males have a lower chance of leaving offspring than hybrid females. Hybrid males either suffer from lower viability or are unable to find a mate. (Grant KBN 6P04C 002 21)

4.19P

DIFFERENTIAL INTROGRESSION OF SEX CHROMOSOMES IN *SILENE*: HALDANE'S RULE IN PLANTS?

Joseph E. Ironside, Dmitry A. Filatov

School of Biosciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK

Plants of section *Elisanthe* (genus *Silene*) are dioecious, with chromosomal sex determination. Recombination between the X- and Y-chromosomes of these species has been suppressed yet many X-linked genes retain functional homologues on the Y-chromosome. The four Elisanthe species *Silene latifolia, S. heuffelii, S. dioica* and *S. diclinis* are interfertile and produce hybrid swarms where they occur in sympatry. We have studied the diversity of X- and Y-linked homologues of the 10kb DD44 gene within these species. Our results indicate that introgression of the X-linked DD44 homologue has occurred among the *Elisanthe* species but that introgression of the Y-linked homologue has not occurred. Together with existing evidence for female-biased hybrid sex ratios from crosses between *Elisanthe* species, these findings suggest that *Elisanthe* Y-chromosomes suffer a greater hybrid disadvantage than X-chromosomes, a possible example of the operation of Haldane's Rule within a naturally hybridizing group of plants.

4.20P

NON-RANDOM SEXUAL REPRODUCTION IN A *DAPHNIA* HYBRID SPECIES COMPLEX: ITS CONSEQUENCES FOR THE RESTING EGG BANK

Barbara Keller, Piet Spaak

EAWAG, Dept. Limnology; Ueberlandstrasse 133, CH-8600 Duebendorf, Switzerland

Sexual reproduction in *Daphnia* gives the opportunity for hybridisation and results in the production of resting eggs, enclosed in a structure called ephippium. By sedimentation ephippia accumulate in the sediment of a lake and can be analyzed over decades, offering the opportunity for microevolutionary studies and for the study of former pelagic populations. In a Swiss subalpine lake (Greifensee), we studied the genetic structure of the pelagic *Daphnia galeata x hyalina* hybrid species complex. We examined sexual females, males and ephippia production. Eggs from ephippia were hatched, genotypes and taxa composition of all daphnids were determined using four polymorphic enzyme loci, two of which are diagnostic. We found significant differences between the genetic composition of the pelagic asexual *Daphnia* population, the sexual females and the ephippial eggs (*Daphnia* hatchlings). Additionally, taxa composition and backcross-levels differed significantly between these three reproductive stages. In contrast to the asexual population, which is dominated by hybrids, sexual females and especially *Daphnia* hatched from ephippial eggs are dominated by *D. galeata* . However, hybrid ephippial females were commonly found in the lake during the observed sexual phases. We conclude that hybrid *Daphnia* have a lower reproductive fitness compared to the parental *D. galeata*. Furthermore, the taxon composition of the resting eggs does not seem to reflect the former population and therefore *Daphnia* resting egg bank does not necessarily represent the past population in the lake.

4.21P

HYBRID BREAKDOWN BETWEEN *DROSOPHILA MADEIRENSIS* AND *DROSOPHILA SUBOBSCURA*

Margarida Matos

Fac. Ciências Univ. Lisboa, Centro de Biologia Ambiental, Departamento de Biologia Animal, 1749-016 Lisboa Portugal

Drosophila madeirensis and *Drosophila subobscura* are two very closely related species, having diverged recently (0.6-1.0 Myr ago) from a common ancestor. *Drosophila subobscura*, typically a Palearctic species, can be found nowadays in the Palearctic, Nearctic and Neotropical biogeographic regions. *Drosophila madeirensis* is an endemic species from Madeira Island associated with Laurissilva forest. This habitat, considered a relic from the tertiary period, is nowadays restricted to some macaronesian islands and some areas in occidental Africa, and is being threatened by human activities. The two species coexist in sympatry in Madeira Island, being morphologically very similar and having an incomplete reproductive isolation. Though there are some studies reporting that hybrids can be obtained under captivity, detailed studies involving the fitness of the hybrid populations are lacking. Two years ago we founded, from collections in Madeira, laboratory populations of both species, three-fold replicated. These species, as well as their hybrids, have been characterized in terms of several life-history traits. F1 hybrids between these species are easily obtained, especially in crosses involving *D. madeirensis* females and *D. subobscura* males. This cross yields similar number of females and males. On the other hand the sex ratio of the reciprocal cross is extremely biased in terms of males (0.81 ± 0.03). In both crosses it is possible to obtain viable and fertile F2 hybrids. This allows to undertake experiments of hybrid breakdown, in order to quantify several variance components involved in the differences between these species. With this in mind, we undertook a hybrid breakdown experiment involving several life history traits. The results of this study will be discussed.

4.22P

THE IMPACT OF HYBRIDISATION ON THE ENDANGERED WILD POPULATIONS OF THE SAKER FALCON (*FALCO CHERRUG*)

[1]Franziska Nittinger, [1]Elisabeth Haring, [2]Wilhelm Pinsker, [1]Anita Gamauf

[1]*Museum of Natural History Vienna, Laboratory of Molecular Systematics, Burgring 7, A-1014 Vienna, Austria*

[2]*Institute of Medical Biology, University of Vienna, Waehringerstr. 10, A-1090 Vienna, Austria*

The impact of man-induced hybridisation on the endangered wild populations of *F. cherrug* is investigated by comparing recent and historical populations. Both fresh samples and museums specimens are analysed from several populations of the Saker Falcon in Eastern Europe, Central and Eastern Asia. Population samples are taken from all classified subspecies and from different parts of the respective geographic distribution ranges. Representatives of other related falcons, which are possible candidates for hybridization, are also included: Gyrfalcon (*F. rusticolus*), Lanner Falcon (*F. biarmicus*), Lagger Falcon (*F. jugger*), Prairie Falcon (*F. mexicanus*), and Peregrine Falcon (*F. peregrinus*). In addition, the phylogenetic relationships of the Saker Falcon and other big falcons are analysed genetically. We present preliminary results of the genetic study and provide data on the efficiency of the various molecular markers to discriminate the closely related taxa. Fragment length polymorphism was studied at ten microsatellite loci and sequence variation was analysed in two non-coding regions of the mitochondrial genome. The data obtained with these two marker systems (nuclear and mitochondrial DNA) are compared.

4.23P

GENE FLOW IN A HOUSE MOUSE CHROMOSOMAL HYBRID ZONE

[1]T. Panithanarak, [1]H. C. Hauffe, [2]J. F. Dallas, [1]J. B. Searle

[1]*Department of Biology, University of York, PO Box 373, YorkYO10 5YW, UK*

[2]*School of Biological Sciences, University of Aberdeen,Tillydrone Avenue, Aberdeen AB24 2TZ, UK*

The West European house mouse (*Mus musculus domesticus*) is subdivided into many chromosomal races. In the alpine valley of Valtellina, Northern Italy, two chromosomal races were described as the Upper Valtellina (UV) with metacentrics 2.8 and 10.12 and the Poschiavo (POS) which carries metacentric 8.12 and acrocentrics 2 and 10. These races produce unfit hybrids due to problems in chromosome pairing and segregation. The races occur together in Sommacologna and Sondalo, but otherwise occur in separate villages in the valley. To study gene flow between these races in Valtellina, we have scored 13 microsatellite loci using 179 mice from 16 villages. Seven of the microsatellite loci were mapped at centromeric regions of chromosomes 10 and 12 that differ between the races. These loci are more likely to display race-specific alleles compared to the other six loci at the telomeres of chromosomes 10 and 12 and at the centromeres of other chromosomes shared between the two races. Considering separated UV and POS populations within the valley, allelic differences between the races were found at five centromeric loci of chromosomes 10 and 12 but at none of the other loci. This distinction was not found in Sommacologna and Sondalo where the UV and POS populations occur in sympatry. These results provide evidence for reduced gene flow at the centromeric regions of race-specific chromosomes in situations where there is not intense interbreeding.

4.24P

GENETIC STRUCTURE OF THE NARROW HYBRID ZONE BETWEEN *SOREX ARANEUS* CHROMOSOME RACES IN POLAND REVEALED BY ALLOZYMES AND MICROSATELLITE DNA

Miroslaw Ratkiewicz, K. Jadwiszczak, A. Banaszek, S. Fedyk

University of Bialystok, Swierkowa 20B, 15-950 Bialystok, Poland

The common shrew, *Sorex araneus* is characterized by the existence of different chromosome races and hybrid zones with multiple opposing clines. Of particular interest is the Bialowieza (Bi) / Drnholec (Dn) hybrid zone in Poland, as it is very narrow (less than 100m) and hybrids with chain meiotic complexes up to 10 elements were recorded there. Genetic structure of the Bi/Dn hybrid zone was analysed using 31 allozyme loci and five microsatellite DNA markers and compared to chromosomal structure of this hybrid zone. The potential role of environmental barrier (high railway embankment) situated in the centre of the zone, as possible obstacle to gene flow was also tested. The results are discussed with those for the other *Sorex araneus* hybrid zones in Europe.

4.25P

ECOLOGICAL CONSEQUENCES OF AN EVOLUTIONARY PROCESS: HYBRIDISATION IN *RORIPPA*

Marc Stift, C. Pieternella, J. Luttikhuizen, Gerard B. Oostermeijer, Hans C. M. Den Nijs, Peter H. van Tienderen

University of Amsterdam, Institute for Biodiversity and Ecosystem Dynamics, P.O. Box 94062, 1090 GB, Amsterdam, The Netherlands

Until recently, hybridisation has been considered to be of minor evolutionary importance, particularly because hybrids seem to have a lower average fitness than their "full" parental species. Indeed, the majority of the hybrid offspring appears to have a lower fertility, which is reflected by a reduced seed set and low germination rates. Therefore, hybridisation seems to be of minor evolutionary importance. On the other hand, numerous polyploid plant species have probably originated from past hybridisation events. This contradiction, together with the increasing number of studies that have shown gene flow between species, suggests hybridisation to be more important than was previously thought. Particularly in plants, hybridisation could actually be an important evolutionary force. Traditionally, reproductive parameters have been used to estimate hybrid fitness. However, fitness is not solely determined by reproductive capacity. Ecological fitness components like survival may be of equal importance. The typical floodplain genus *Rorippa* has three Dutch representatives, each occupying a different niche, reflected in a different strategy to survive flooding. Hybridisation between the species readily occurs in the wild, giving rise to the question as to what the flooding strategy of hybrids will be. In this study we focus on the *R. x anceps* hybrid complex (*R. amphibia* x *R. sylvestris*). In greenhouse experiments we will compare both reproductive and ecological fitness components of the F1 hybrids, the first backcross generation and the parents. Along with this experimental work, we will use molecular markers to establish the frequency and distribution of hybrids in wild populations. Our main goal is to establish the ecological and evolutionary significance of hybridisation in *Rorippa*.

4.26P

NATURAL HYBRIDIZATION BETWEEN TWO *RHINANTHUS* SPECIES

Renate A. Wesselingh, Véronique Ducarme

[1] *Biodiversity Research Centre, Université catholique de Louvain, Croix du Sud 4-5, B-1348 Louvain-la-Neuve, Belgium*

Rhinanthus (Scrophulariaceae) is a European genus of annual hemiparasitic herbs found in extensively managed hay meadows. Among the 25 species known, many species pairs have been reported as interfertile. We study in detail the processes involved in hybridization between *R. minor* and *R. angustifolius*, two widely distributed species with overlapping habitat requirements. We are interested in both the onset of hybridization in mixed populations and the fate of these populations in the long run. We follow mixed populations over time using species-specific molecular markers. We aim to analyse in detail the behaviour of bumblebee pollinators in relation to relative densities and spatial arrangement of each of the parental species (with and without the addition of hybrid individuals), in order to model pollen flow between the species. Controlled crosses in the greenhouse yield data concerning the relative success of interspecific pollinations (seed set, germination), and field trials will be carried out to determine the relative fitness of known hybrid genotypes.

Symposium 5

Evolution in non-coding DNA

Organisers: Richard Sibly & Mark Pagel

Roger Stevens Lecture Theatre 22

09.50 – 10.20	**Hartl, D. L.** Genomic Themes in Augmented and Diminished C
10.20 – 11.00	**Coffee**
11.00 – 11.30	**Li, W-H.** Methods for analyzing genomic DNA sequences
11.30 – 12.00	**Tristem, M.** The evolution, persistence and distribution of endogenous retroviruses
12.00 – 12.20	**Brookfield, J. F. Y.** Phylogenies of interspersed repetitive DNA families when not all copies are active
12.20 – 12.40	**Johnson, L.** Sequence analysis of rodent ID elements: Re-assessing the evidence for a master gene
12.40 – 14.00	**Lunch**
14.00 – 14.20	**Papp, B.** Dosage sensitivity and evolution of gene co-regulation and gene families yeast
14.20 – 14.40	**Keightley, P. D.** Quantifying functional constraints in noncoding DNA
14.40 – 15.00	**Parsch, J.** Selective constraints on intron evolution in Drosophila
15.00 – 15. 20	**Sibly, R. M.** In search of a general theory of microsatellite evolution
15.20 – 16.00	**Tea**
16.00 – 16.20	**Weetman, D.** Misbehaving microsatellites: how significant are deviations from classical mutation models?
16.20 – 16.40	**Ustinova, J.** Length and frequency of microsatellite loci in the huge genome of the acridid grasshopper *Chorthippus biguttulus*
16.40 – 17. 00	**Meagher, T. R.** QTLs need not be coding loci - localised variation in DNA content within the genome of *Silene latifolia*
17.00 – 17.20	**Filatov, D. A.** Molecular evolution of the human pseudoautosomal region

Invited talks

5.1

GENOMIC THEMES IN AUGMENTED AND DIMINISHED C

Daniel L. Hartl, Elena R. Lozovsky, Justin Blumenstiel.

Harvard University, Cambridge, MA

Genome size is ultimately determined by multiple interacting factors including the frequency and average size of spontaneous deletions and insertions (indel spectrum). Large differences observed in indel spectra of organisms as diverse as *Drosophila*, nematodes, crickets, grasshoppers, and mammals have led to the suggestion that spontaneous deletions and insertions may have important implications for genome evolution with regard to the persistence of pseudogenes and other expendable sequences whose length is not constrained, or only weakly constrained, by selection. To check for possible biases resulting from the types of sequences analyzed, we have investigated whether indel spectra differ across families of transposable elements, classes of genomic sequences (e.g., repetitive versus unique) or chromatin domains (e.g., heterochromatin versus euchromatin). We have analyzed the indel spectrum in all euchromatic and heterochromatic insertions of the non-LTR retrotransposable elements *Helena, Jockey, Waldo, X* and *You* present in *D. melanogaster*. We also cloned and sequenced *Helena* copies from *D. virilis*, and identified them as euchromatic or heterochromatic insertions. These data yielded comparisons of indel spectra across the different transposons and between euchromatin and heterochromatin. The data suggests bursts of transposition of individual elements, approximately equality of the indel spectra across different chromatin domains, and relatively long-term persistence of transposable elements in heterochromatin.

5.2

METHODS FOR ANALYZING GENOMIC DNA SEQUENCES

LI WEN-HSIUNG

University of Chicago, 1101 East 57th Street, Chicago, IL 60637

The first step in comparative analysis of genomic sequences is usually sequence alignment. Aligning genomic sequences is much more difficult than aligning coding or protein sequences because genomic sequences are much longer than coding sequences and often have been scrambled by deletions, insertions, and other genomic rearrangements. Thus, traditional methods of alignment are not suitable for this purpose. I shall present a novel method for aligning genomic sequences. I shall also present a method for distinguishing between coding and non-coding sequences.

5.3

THE EVOLUTION, PERSISTENCE AND DISTRIBUTION OF ENDOGENOUS RETROVIRUSES

Mike Tristem

Department of Biological Sciences Silwood Park Ascot Berkshire SL5 7PY United Kingdom

One subset of selfish genetic elements present within vertebrate genomes are endogenous retroviruses (ERVs), which within humans account for perhaps 8% of the total size of the genome. ERVs within humans are classified into families with each family resulting from the integration of a single 'founder' virus from another species. We know that, in general, once a novel retrovirus has been integrated retrotransposition results in an increase in copy number, and thus the human endogenous retrovirus (HERV) families have copy numbers varying from between one and many hundreds. Horizontal transmission of ERVs occurs frequently between different species, but is nevertheless strongly constrained by the phylogenetic distance between hosts, and probably also by the genotypes of the viruses themselves. The human genome sequence has allowed us, for the first time, to investigate ERV evolution in detail. There are over 30 independently derived HERV families and valuable insights have already been gained into their long-term retrotranspositional dynamics, as well as factors affecting their persistence, genomic distribution and occasional domestication by their hosts. In the future it is expected that an increasing use will be made of additional whole genome sequences, and this will allow us to compare and contrast the evolution of ERVs in hosts with different life-histories.

Contributed talks

5.4

PHYLOGENIES OF INTERSPERSED REPETITIVE DNA FAMILIES WHEN NOT ALL COPIES ARE ACTIVE.

John F.Y. Brookfield, Louise J. Johnson

Institute of Genetics, University of Nottingham, Queens Medical Centre, Nottingham, NG7 2UH

Interspersed repetitive DNA sequences within a genome are connected by a phylogeny. Some have interpreted the phylogenetic patterns observed as representing those expected when there are only a few "Master genes" that are the source of all transposition. We consider, using a coalescent approach, the expected phylogenies expected at equilibrium under models of mobile DNAs when most elements have become inactivated, either at the moment of transposition or by random mutation at other times. We show that, even when the number of active elements is large, but less than the square root of the total number of elements, the phylogeny connecting elements may resemble that expected with a single master gene. This is particularly expected when the host's population size is small. We also consider the impact on expected phylogenies of mutations conferring increased transposition rates on individual element copies. We also examine expected effects of deviations from equilibrium. The models are considered in conjunction with data from mammalian interspersed repetitive DNA sequence families.

5.5

SEQUENCE ANALYSIS OF RODENT ID ELEMENTS: RE-ASSESSING THE EVIDENCE FOR A MASTER GENE.

Louise Johnson, John F. Y. Brookfield

University of Nottingham, Queens Medical Centre, Nottingham NG7 2UH

Many families of interspersed repetitive DNA elements, including human Alu and LINE elements, have been proposed to have accumulated through repeated copying from a single source locus: the 'master gene'. Rodent ID elements are one of the best-supported examples of this 'master gene' style expansion. In mouse, indirect but persuasive evidence points to the BC1 gene as the major source of new elements and BC1 has therefore been presumed to be the master gene in mouse and other rodents, although in the rat it is evident that another transpositional source is active. Here we analyse rodent ID element sequences to assess the evidence for non-master gene replication.

5.6

DOSAGE SENSITIVITY AND EVOLUTION OF GENE CO-REGULATION AND GENE FAMILIES YEAST.

B. Papp, C. Pál, L.D. Hurst, Loránd Eötvös

University, Pázmány sétány 1/C, 1117 Budapest, Hungary

University of Bath, Claverton Down, BA2 7AY Bath, UK.

According to what we term the balance hypothesis, an imbalance in the concentration of the sub-components of a protein-protein complex can be deleterious. If so, a) both under and over-expression of protein complex subunits should lower fitness and b) accuracy of transcriptional co-regulation of subunits should reflect the extent of deleterious consequences of imbalance. Here we show that all these predictions are upheld in yeast (*Saccharomyces cerevisiae*). This supports the physiological theory for the origin of dominance. Beyond this, single gene duplication of protein subunits is expected to be harmful, as this too leads to imbalance. Indeed, members of large gene families are rarely involved in complexes. The balance hypothesis thus provides a single theoretical framework for understanding both dominance and gene family size.

5.7

QUANTIFYING FUNCTIONAL CONSTRAINTS IN NONCODING DNA.

P. D Keightley, T. Johnson, D. J. Gaffney

University of Edinburgh, School of Biological Sciences, Ashworth Laboratories, West Mains Road, Edinburgh EH9 3JT, UK

We estimate levels of evolutionary constraint, the fraction of point mutations that are subject to purifying selection, in noncoding DNA by comparing rates of substitution at synonymous sites of orthologous genes with rates of substitution in adjacent noncoding DNA. In aligning noncoding DNA sequences, indel patterns are ambiguous, so we have developed a new Monte Carlo alignment method that is based on an evolutionary model of insertion/deletion (indel) evolution. Alignment is estimated as a function of rates of indels relative to nucleotide substitutions, and the length distribution of indels, and these parameters are specific to the taxonomic group in question. In both *Drosophila* and rodent introns, constraint is close to zero, with the exception of short runs of nucleotides close to the 5' and 3' splice sequences. In contrast, noncoding DNA segments upstream and downstream from the start and stop codons show moderately strong constraint: an average of 30-40% of point mutations are eliminated by selection close to the 5' and 3' ends of genes. In rodents, conservation extends for an average of more than 1kb in either direction from coding sequences. Deleterious mutations in noncoding DNA appear to make a substantial contribution to the mutation load in both rodents and *Drosophila*.

5.8

SELECTIVE CONSTRAINTS ON INTRON EVOLUTION IN *DROSOPHILA*.

John Parsch

University of Munich Department of Biology II, Luisenstr. 14, 80333 Munich, Germany

Intron sizes show an asymmetrical distribution in a number of organisms, with a large number of "short" introns clustered around a minimal intron length and a much broader distribution of longer introns. In *Drosophila melanogaster*, the short intron class is centered around 61 ± 10 bp. The narrow length distribution of this class of introns suggests that natural selection may play a role in maintaining intron size. A comparison of 15 orthologous introns among eight species of the *D. melanogaster* species subgroup indicates that, in general, short introns are not under greater DNA sequence or length constraints than long introns. There is a bias towards deletions in all introns (deletion/insertion ratio = 1.66), and the vast majority of all indels are of short length (< 10 bp). Indels occurring on the internal branches of the phylogenetic tree are significantly longer than those occurring on the terminal branches. These results are consistent with a compensatory model of intron length evolution in which slightly deleterious short deletions are frequently fixed within species by genetic drift, and relatively rare larger insertions that restore intron length are fixed by positive selection. A comparison of paralogous introns shared among duplicated genes suggests that length constraints may differ between introns within the same gene. The *janusA*, *janusB*, and *ocnus* genes share two short introns derived from a common ancestor. The first of these introns shows significantly fewer indels than the second, though the two introns show a comparable number of base substitutions. This indicates that intron-specific selective constraints have been maintained following gene duplication, which preceded the divergence of the *D. melanogaster* species subgroup.

5.9

IN SEARCH OF A GENERAL THEORY OF MICROSATELLITE EVOLUTION.

Richard M. Sibly

School of Animal and Microbial Sciences, University of Reading RG6 6AJ, UK

Microsatellite lengths change over evolutionary time through a process of replication slippage. A recently proposed model of this process holds that the expansionary tendencies of slippage mutation are balanced by point mutations breaking longer microsatellites into smaller units, and that this process gives rise to the observed frequency distributions of uninterrupted microsatellite lengths. This theory has the attraction of providing a mechanistic account of the evolutionary process but some of its predictions are wrong. The alternative theory supposes that longer microsatellites experience more contractions than expansions, so that there is a length-dependant mutation bias. This theory lacks a mechanistic basis but some of its predictions are wrong too. Where do we go from here?

5.10

MISBEHAVING MICROSATELLITES: HOW SIGNIFICANT ARE DEVIATIONS FROM CLASSICAL MUTATION MODELS?

David Weetman

University of Hull, Department of Biological Sciences, Hull HU6 7RX UK

Microsatellites are used as genetic markers in a wide range of studies, and most of these analyses rely on the assumption of an underlying mutation model. The two most commonly assumed, the Infinite Alleles Model and the (strict) Stewise Mutation Model, are mathematically tractable, but are now known to represent considerable oversimplifications of microsatellite mutation processes. Progress has recently been made in determining the consequences of deviation from IAM/ SMM assumptions for particular measures of genetic distance. Thus with knowledge of how microsatellites applied in a study may violate IAM or SMM properties, it may be possible to predict the performance of different analytical tools. Unfortunately, although microsatellites are used in studies of a diverse range of organisms, their mutation processes have been investigated in few, and so predictions will rely on the availability and efficacy of general mutational rules-of-thumb for different types of loci and taxa. Here I review published data on a major aspect of the microsatellite mutation process: the size spectrum of mutations. Early studies suggested a closer fit to the SMM than IAM, and it is frequently stated, sometimes without support, that most microsatellite mutations are single steps. However a major finding of the review is that whilst across studies the mean proportion of mutations larger than single steps is quite low, high variability exists both between and, most strikingly, within studies, so undermining the SMM. The robustness of this conclusion, and the possible existence of taxon-specific step-size spectra, are examined with respect to the reliability of the different types of analyses employed by the studies included in the review. Finally, the significance of such apparent deviations from the mutation model assumptions for microsatellite-based analyses are assessed in the light of several recently-published theoretical analyses.

5.11

LENGTH AND FREQUENCY OF MICROSATELLITE LOCI IN THE HUGE GENOME OF THE ACRIDID GRASSHOPPER *CHORTHIPPUS BIGUTTULUS.*

Jana Ustinova, Sylvia Cremer, Frieder Mayer

University of Erlangen, Institute of Zoology II, Staudtstr. 5, 91058 Erlangen, Germany

It is commonly believed that both the average length and frequency of microsatellites correlate with genome size. Among animals, insects tend to have shorter loci when compared to vertebrates. However, previous studies concentrated on species with small genome sizes. We have studied frequency and average locus lengths for 64 di- and 15 trinucleotide microsatellite loci of the insect with an exceptionally large genome, *Chorthippus biguttulus* (Orthoptera, Acrididae). Microsatellites are not more frequent in *C. biguttulus* but dinucleotide repeats are longer than in other studied insect species. The average dinucleotide locus length lies in the range of higher vertebrates. Dinucleotide loci make up about one percent of the genome of *C. biguttulus* , what is at least 2.5 times higher than by *Drosophila melanogaster*. In addition, we have studied allelic variation at some di- and trinucleotide microsatellite loci in natural populations, and have found that dinucleotide loci are extremely variable, with numerous null alleles. We speculate that the difficulties in amplification of these loci are caused by a combination of the huge genome size and the length of dinucleotide repeats.

5.12

QTLS NEED NOT BE CODING LOCI - LOCALISED VARIATION IN DNA CONTENT WITHIN THE GENOME OF *SILENE LATIFOLIA*.

Thomas R. Meagher, Denise E. Costich, Amanda C. M. Gillies

University of St Andrews, Sir Harold Mitchell Building, St Andrews KY16 9TH, United Kingdom.

DNA content variation, attributed to variation in non-coding DNA, has long been known to be related to adaptation. More recently, our lab demonstrated that variation in non-coding DNA content underlies response to short-term selection on ecologically relevant characters, notable flower size in *Silene latifolia*. Such characters are typically studied using the methodology of quantitative genetics, which in turn presumes the existence of underlying coding loci. Our results showed that non-coding DNA may play a much larger role in quantitative trait variation and response to selection than previously realised. The present talk presents results of an investigation of chromosomal location of quantitative trait loci (QTL) underlying floral variation and DNA content using an AFLP-based genetic map. Two hundred ninety one progeny from a cross between male and female plants of *S. latifolia* were measured for floral dimensions, nuclear DNA content based on flow cytometry, and AFLP markers based on 15 primer pair combinations. The resulting data were used to construct male- and female-specific genetic maps within which the location and magnitudes of QTL for floral dimensions and DNA content were investigated. The objective of this study was to determine the precise relationship between localised DNA content and phenotypic variation in quantitative traits. Our analyses revealed a strong negative correlation (-0.88) between magnitudes of QTL effects on DNA content and flower calyx diameter. These results support our earlier finding that DNA content is an important factor in phenotypic evolution, and more specifically show that QTLs may result from localised features of genome organization rather than coding loci per se.

5.13

MOLECULAR EVOLUTION OF THE HUMAN PSEUDOAUTOSOMAL REGION.

Dmitry A. Filatov, Ravinder Kanda.

University of Birmingham, School of Biosciences, Edgbaston, Birmingham B15 2TT, United Kingdom

Recombination was suggested to be mutagenic *per se*. Here we present sequence diversity and divergence data from the human and ape p-arm pseudoautosomal region (p-PAR), which corroborates this hypothesis. It has been demonstrated that recombination in this region is at least twenty times more frequent than the genomic average of ~1 cM/Mb. If recombination is mutagenic, this is expected to result in a high mutation rate in this region and elevated intraspecies diversity and interspecies silent divergence. Here we report the analysis of DNA diversity and substitution patterns and rates in six genes spanning a proximal megabase of the p-PAR. Between species silent divergence in the PAR forms a gradient, with the distal PAR region diverging significantly faster than the proximal 0.2Mb and than the non-PAR genes. We hypothesize that this gradient is due to a mutagenic effect of recombination, which is very frequent in the distal PAR and might be lower near the PAR boundary, resembling suppression of recombination in the proximity of chromosomal inversions.

Posters

5.14P

A TEST OF THE POSSIBLE REDUCTION IN MUTATION RATE OF THE AVIAN Z CHROMOSOME

Erik Axelsson, Nick Smith, Hannah Sundström, Sofia Berlin, Hans Ellegren

Uppsala University, Evolutionary Biology Centre, Norbyvaegen 18 D, 752 36 Uppsala, Sweden

In mammals, a greater divergence Y-chromosome as compared to X-chromosome sequences has generally been seen as evidence for a male-biased mutation rate. However, the fact that X is present as a single copy in males, and that deleterious mutations thereby will be exposed has led to the idea that the X chromosome mutation rate may be specifically reduced. If so, estimates of the male-to-female mutation rate ratio based on X-Y comparison may be flawed. To address this issue we have chosen to study avian sex chromosome divergence, which should be advantageous as birds have female heterogamety (males ZZ, females ZW). In birds, Z evolves faster than W due to male-biased mutation, and should thus also be expected to evolve somewhat faster than autosomes. However, if the Z chromosome mutation rate is also reduced, we shall expected Z to evolve slower than autosomes. We compared the intronic substitution rate between a large number of Z-linked and autosomal genes, by sequence analysis of chicken and turkey. There was no clear difference in the mean substitution rates of Z-linked and autosomal genes, indicating that any reduction in the Z chromosome mutation rate can only be modest, at most.

5.15P

LIFE HISTORY AND THE MALE MUTATION BIAS

S. Berlin, A. Bartosch-Harlid, N. G. C. Smith, A. P. Møller, H. Ellegren

Uppsala University, Norbyvagen 18D, 75236 Uppsala, Sweden

If DNA replication is a major cause of mutation, then those life history characters, which are expected to affect the number of male germline cell divisions, should also affect the male to female mutation bias (alpha). We tested this hypothesis by comparing several clades of bird species, which show variation both in suitable life history characters (generation time as measured by age at first breeding and sexual selection as measured by frequency of extra pair paternity) and in alpha, which was estimated by comparing Z-linked and W-linked substitution rates in paralogous introns. Alpha differences between clades were found to positively covary with both generation time and sexual selection as expected if DNA replication causes mutation. The effects of extra pair paternity frequency on alpha suggests that increased levels of sexual selection cause higher mutation rates, which offers an interesting solution to the paradox of the loss of genetic variance associated with strong directional sexual selection. We also used relative rate tests to examine whether the observed differences in alpha between clades were due to differences in W-linked or Z-linked substitution rates. In one case a significant difference in alpha between two clades was shown to be due to W-linked rates and not Z-linked rates, a result which suggests that mutation rates are not determined by replication alone.

5.16P

SELECTIVE SWEEPS AT Z-LINKED LOCI IN *FICEDULA* FLYCATCHERS

T. Borge, M.T. Webster, G. Andersson, G-P Sætre

Uppsala University, EBC, Department of Evolutionary Biology, Norbyvägen 18d, SE-752 36 Uppsala, Sweden

Positive selection reduces natural sequence variation both in the selected region and at surrounding linked sites. Selective sweeps at sex-linked genes have been suggested to cause reduced sequence variation in the Z-chromosome in birds. In order to discriminate between positive selection and other factors that can affect genetic diversity, we surveyed about 10 kb of intronic DNA from nine Z-linked genes in several individuals from two *Ficedula* flycatcher species (*Ficedula hypoleuca* and *F. albicollis*). Average variation on the Z-chromosome in both species is significantly lower than predicted from autosomal diversity. Furthermore, there is a marked heterogeneity in levels of polymorphism at different loci between the two species, consistent with the effects of episodic selective sweeps. We conclude that high levels of positive selection have characterized the evolution of the Z-chromosome in *Ficedula* flycatchers.

5.17P

LIVE WITHOUT NON-CODING DNA: ANALYSIS OF A PILOT GENOME PROJECT OF *OXYTRICHA TRIFALLAX*'S SOMATIC NUCLEUS

Andre R.O. Cavalcanti, Tom Doak, Glen Herrick, Robert Weiss, Laura Landweber

Princeton University, Dept. of Ecology and Evolutionary Biology, Princeton, NJ, USA

Live without non-coding DNA: Analysis of a pilot genome project of *Oxytricha trifallax*'s somatic nucleus. Ciliates are an unusual group of microbial eukaryotes. They all possess two types of nuclei - a somatic macronucleus (MAC), responsible for most RNA synthesis, and a germline micronucleus (MIC), responsible for genetic exchange in sexual reproduction. Massive DNA cleavage, rearrangement and amplification are required to form the new MAC genome from the MIC after sexual exchange. In *Oxytricha trifallax*, after all DNA processing, the newly formed MAC is almost devoid of non-coding DNA, and is composed of about ~24,000 kinds of gene-sized molecules (individual coding regions packaged with their regulatory sequences and telomeres), each ~2kb long and present in ~1000 copies. The organization of the somatic genome in "nano-chromosomes" should facilitate both sequencing and annotation of the entire 50 Mb MAC genome (the ensemble of such molecules), with very little non-coding DNA and no need for assembly. Scrambled genes, assembled from disperse gene-fragments in the MIC, are an added layer of complexity to spirotrich genomes. *Oxytricha trifallax* was recently added to NHGRI's high-priority list of model organisms for genome sequencing. Several results from the pilot study will be discussed.

5.18P

DIVERSITY IN THE HUMAN PSEUDOAUTOSOMAL REGION

R. Kanda, D. Filatov

School of Biosciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT

Human X and Y chromosomes recombine in two pseudoautosomal regions (PARs), located at either ends of the sex chromosomes. The shorter arms of the sex chromosomes (Xp/Yp) contain the larger p-PAR, approximately 2.6Mb in size, and recombination in this region is essential for correct segregation of the sex chromosomes in male meiosis, resulting in a recombination rate in this region greater than 20 times the genomic average. Experimental evidence in yeast would suggest that recombination may be responsible for a substantial increase in the mutation rate. Under this scenario, one would expect elevated levels of diversity within species in the PAR. However, there is also evidence that recombination may affect substitution patterns and rates. It has been demonstrated that in yeast and mammalian cells resolution of mismatched heteroduplexes ((A or T)/(G or C)), formed during recombination, is biased towards GC (biased gene conversion, BGC). AS BGC is more frequent in recombinational hotspots, one would anticipate a higher GC content in the PAR. BGC has been demonstrated to be equivalent to selection for (A or T) =>(G or C) mutations, which would imply an increase in the number of (A or T) =>(G or C) substitutions and a reduction in the number of substitutions in the opposite direction, resulting in a substantial overall reduction in the substitution rate in GC rich regions. Under these circumstances, one would anticipate reduced levels of diversity within species in the PAR, in contrast with the idea of recombination being mutagenic. Here we present DNA diversity data from several p-PAR regions which demonstrate significantly elevated levels of diversity within humans, in support of the 1st hypothesis. However, the comparison between (A or T)/(G or C) and A/T or G/C polymorphic sites suggest a role for BGC in the PAR.

5.19P

HERV-K (HML-2) POLYMORPHISMS AS MARKERS FOR EXAMINING HUMAN EVOLUTION AND EXPANION

C. M. Macfarlane, P. Simmonds

Virus Evolution Group, Laboratories of Clinical and Molecular Virology University of Edinburgh, Summerhall, EH9 1QH Scotland

HERV-K (HML-2) is acknowledged to be the most biologically active human endogenous retrovirus family and contains germ cell insertions that post-date the human / chimpanzee split. The identification of polymorphic HERV-K (HML-2) integrations or subsequent mutations that lead to the production of a solitary LTR (long terminal repeat) are useful for examining hominid evolution as they represent a unique event, are identical by descent and have a known ancestral state. We have compiled a catalogue of all HERV-K (HML-2) integrations that are unique to contemporary humans and resolved discrepancies by sequence alignment and assigned chromosomal location. From the total of 63, we selected 9 elements that did not appear to have undergone inter-element recombination and were evolutionary recent. We designed PCR assays to test for the presence or absence of the HERV-K (HML-2) integration and for the production of a solitary LTR at each locus. A total of 107 individuals consisting of: 25 Africans; 27 Asians; 21 Europeans and 34 Papua New Guineans were tested for polymorphism at each of the selected HERV-K (HML-2) loci. Our results indicate a recent African origin and expansion of contemporary humans, with the complete replacement of 'archaic' sapiens populations throughout the world.

5.20P

MOLECULAR PHYLOGENY OF DOLICHOPODA CAVE CRICKETS AND THE MODE OF EVOLUTION OF THE PDO500 SATELLITE DNA FAMILY

Lene Martinsen, Federica Venanzetti, Lutz Bachmann

Natural History Museums and Botanical Garden, Section for Zoology, University of Oslo

Cave crickets of the genus *Dolichopoda* (Orthoptera, Rhaphidophoridae) are patchily distributed throughout the North Mediterranean regions. The high degree of geographical isolation might allow insights into the short-term processes of genetic differentiation of *Dolichopoda* populations and species, and the mode of evolution of rapidly evolving genome components such as e.g. tandemly repeated non-coding satellite DNA can be studied in detail. So far, three specific satellite DNA families have been described in *D. schiavazzii.* The pDoP102 and pDsPv400 satellite DNA families are species specific while the pDo500 family is present in the genomes of all *Dolichopoda* species analyzed. The copy number and the intraspecific sequence diversity of pDoP102 and pDsPv400 are high, indicating a high evolutionary turnover of both sequence family. In contrast, the interspecific diversity of pDo500 sequences suggests a rather slow mode of evolution. The pDo500 data were mapped on a mitochondrial DNA based phylogeny of the genus allowing for a calibration of its evolutionary rate. Phylogenetic trees deduced from mitochondrial and pDo500 data are basically congruent indicating that pDO500 sequences evolve gradually through the accumulation of single nucleotide substitutions. A detailed analysis of pDo500 characteristics will be presented.

5.21P

FAMILIES OF LTR-RETROTRANSPOSONS IN THE *ARABIDOPSIS* GENOME HAVE DISTINCT TRANSPOSITIONAL HISTORIES

Vini Pereira

Imperial College London, Silwood Park campus, Buckhurst Rd, Ascot, Berkshire SL5 7PY, UK

LTR-retrotransposons have widely colonized the genomes of plants and other eukaryotes. Plant genomes have in many cases been profoundly affected by their presence. The mechanisms that regulated the co-evolution of host and LTR-retrotransposon genomes are not yet fully understood. The availability of sequence data for whole genomes makes it possible to investigate temporal and spatial patterns of retrotranspositional activity. Here I present the results of a genome-wide, computer based palaeontology of LTR-retrotransposon insertions in the *Arabidopsis thaliana* genome. The methodology developed here involves: i) Large-scale mining of chromosomal sequences for the presence LTR fossils. ii) De-fragmentation of elements and identification of intra-element LTR pairs. A pattern-identification algorithm was designed to identify multiple internal fragments and pairs of LTRs corresponding to *single* insertion events. iii) Alignment of pairs of intra-element LTRs and estimation of the age of insertion of these elements from their LTR sequence divergence. Approximately 6,000 LTR-retrotransposon fragments were located, mostly concentrated in the paracentromeric regions. Using the synonymous substitution rate that has been previously calculated for Arabidopsis (0.015 substitutions per site per Myr), I found that most of ~600 elements retaining (at least part of) both their LTRs have inserted in the last 6 million years. The *Athila* superfamily of retroviral-like elements is represented in ~50% of such elements, followed by ~22% of *copia*-like elements. The age distributions of these two groups of elements are significantly different. The distribution for the *Athila* insertions peaked at ~1.5 million years ago, declining in number since, whilst most *copia* elements (35 of which have identical LTRs) are estimated to have inserted in the last 500,000 years.

5.22P

EVOLUTIONARY DYNAMICS OF SATELLITE DNAS IN SOME COLEOPTERAN GENERA

Durdica Ugarkovic, Brankica Mravinac, Branka Bruvo, Nevenka Mestrovic, Miroslav Plohl, Boskovic Ruder

Institute, Bijenicka 54, 10000 Zagreb, Croatia

Different satellite DNAs coexist in the genome forming a set called the satellite DNA library. Within a library satellite DNAs evolve in nucleotide sequence and in copy number. We have studied the evolutionary dynamics of two different satellites PRAT and PMON in the genera *Palorus* and *Pimelia* (Tenebrionidae, Coleoptera). PRAT is present as a highly abundant satellite in the species *Palorus ratzeburgii* and as a low copy number satellite in other congeneric species. This satellite is also detected in species from the related genera *Tenebrio* and *Tribolium* as well as in the more distant genus *Pimelia*. The comparison of PRAT sequences from different species reveals a high degree of sequence conservation. The mutations profiles are very similar, containing mostly ancestral mutations while species specific mutations are absent even in *Pimelia* species, although the genera *Palorus* and *Pimelia* are separated by 50-60 Myr. The other satellite family, PMON, is spread among all tested *Pimelia* species ranging from highly abundant to low copy number sequence. The PMON sequence is diverging gradually, mostly due to the accumulation of single point mutations. These mutations are not fixed at the level of species but are species-group specific. The PMON satellite is not detected outside of the genus *Pimelia* probably due to sequence divergence beyond recognition. The results reveal that the two satellite DNAs coexisting in some of the species behave as mutually independent evolutionary units, exhibiting different dynamics of sequence change. The dynamics of sequence change seems to be independent of the host species: PRAT satellite sequence is conserved between the analysed species, while PMON is accumulating changes gradually following species phylogeny. The observed high sequence conservation of the PRAT satellite might be induced by a bias of turnover mechanisms, or could indicate functional constraints.

5.23P

MULTI-COPY MICROSATELLITE EVOLUTION

Arjen E. Van 't Hof, Bas J. Zwaan, Paul M. Brakefield

Leiden University, IBL/Evolutionary Biology, P.O. box 9516, 2300 RA Leiden,
The Netherlands

Microsatellites are considered almost exclusively as a molecular tool in most Evolutionary and Ecological studies. Once they are available, only the variation in length and no longer the sequence itself is of interest. They are usually obtained from a single individual, giving at the most 2 different sequences in a diploid organism. In some cases, microsatellites are embedded in transposable elements which occur in many copies throughout the genome. For the researcher who is only interested in the tool, this can be a nightmare, but having large numbers of these sequences available allows a closer look at the dynamics of these still not fully understood repeat groups. The number of accumulated mutation events for a group of multi-copy microsatellites is much higher per generation and per individual than through linear transmission to offspring. Therefore, it is possible to study the evolutionary dynamics of certain sequences within a single individual. The available data from the tropical butterfly *Bicyclus anynana* will contribute in a new way to the ongoing debate about slipped strand mispairing (slippage) versus infinite alleles model mediated trough unequal crossing over. The widespread assumption that flanking sequences of these repeats have very low mutation rates is not supported by this dataset. Furthermore, despite the far above average number of repeats found, there is no evidence for the "growth and collapse" theory which explains the bias towards increase in repeat numbers combined with the absence of large microsatellites.

5.24P

GENOMIC ANALYSIS OF THE RELATIONSHIP BETWEEN REPETITIVE DNA AND PHENOTYPIC EVOLUTION

C. Vassiliadis, T.R. Meagher

University of St Andrews, Sir Harold Mitchell Building St Andrews, Fife KY16 9TH, UK

One revelation of genomics is the evolutionary importance of non-coding DNA sequences. Previous work on *Silene latifolia* by Meagher et al. showed that variation in nuclear DNA content, attributable to non-coding DNA, was negatively correlated with flower size. Other recent investigations of the *Silene latifolia* genome have generated an extensive array of non-coding DNA sequences (e.g. microsatellites, retrotransposons, etc.) that are candidates for investigation of their phenotypic effects. We are presently using *in situ* hybridisation probes of non-coding DNA sequences to explore their distribution and abundance in the *S. latifolia* genome, as well as their relative contribution to phenotype variation. This study is providing new insight into the role of non-coding DNA in phenotypic evolution.

Symposium 6
Sexual conflict
Organisers: Rhonda Snook & David Hosken

Roger Stevens Lecture Theatre 21

09.50 – 10.20	**Arnqvist, G.** Sexual conflict: concepts and empirical avenues
10.20 – 11.00	**Coffee**
11.00 – 11.30	**Eberhard, B.** Male-female conflict and genitalia: failure to confirm predictions
11.30 – 12.00	**Lessells, K.** Why are copulating males bad for females?
12.00 – 12.20	**Moore, P. J.** Patterns of genetic correlations between traits required for male fertility and manipulation of female remating
12.20 – 12.40	**Rodríguez-Muñoz, R.** Genetic trade-offs in fitness related traits in the field cricket *Gryllus bimaculatus*?
12.40 – 14.00	**Lunch**
14.00 – 14.20	**Crudgington H. S.** Experimental removal and elevation of sexual selection in a sperm heteromorphic model insect system: Does sexual selection generate sexual conflict?
14.20 – 14.40	**Wigby, S. L.** The evolution of sexual conflict in *Drosophila melanogaster*
14.40 – 15.00	**Rowe, L.** On detecting sexually antagonistic coevolution with population crosses
15.00 – 15. 20	**Reinhardt, K.** Sexual conflict and reproductive isolation in a hybrid zone
15.20 – 16.00	**Tea**
16.00 – 16.20	**Stockley, P.** Sexual conflict and speciation in rodents
16.20 – 16.40	**Maklakov, A. A.** Conflict and cooperation in mating systems of *Stegodyphusi* spiders
16.40 – 17. 00	**Anthes, N.** Do internally fertilising simultaneous hermaphrodites really trade sperm?
17.00 – 17.20	**Harris W. E.** Sexual conflict. polygyny and female mate preference: avoidance of sperm-depleted males by a novel mechanism of mate discrimination

Invited Talks

6.1

SEXUAL CONFLICT: CONCEPTS AND EMPIRICAL AVENUES

Göran Arnqvist

Dept. Of Animal Ecology, Evolutionary Biology Centre, University of Uppsala, Sweden.

Sexual conflict is currently being studied on something which can be described as a "holey conceptual landscape". Thinking in this field has progressed along several related, but fairly isolated, lines and the theoretical foundation is incomplete. I will discuss a few basic concepts and suggest ways in which current confusion can be reduced. I will also review the empirical methods which have been employed in studies of sexual conflict, and discuss their strengths and weaknesses.

6.2

MALE-FEMALE CONFLICT AND GENITALIA: FAILURE TO CONFIRM PREDICTIONS.

William G Eberhard

Escuela de Biologia, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica

Some recent models suggest a new role for evolutionary arms races between males and females in sexual selection. Female resistance to males is proposed to be driven by the direct advantage to the female of avoiding male-imposed reductions in the number of offspring she can produce, rather than by the indirect advantage of selecting among possible sires for her offspring, as in some traditional models of sexual selection by female choice. This talk is based on the massive but hitherto under-utilized taxonomic literature on genitalic evolution to test, in a two-step process, whether such new models of arms races between males and females have been responsible for rapid divergent evolution of male genitalia. The test revolves around the prediction that "new arms races" are less likely to occur in species in which females are largely or completely protected from unwanted sexual attentions from males (e.g. species which mate in leks or in male swarms, in which males attract females from a distance, or in which females initiate contact by attracting males from a distance). The multiple possible mechanical functions of male genitalia are summarized, and functions of male genitalic structures in 43 species in 21 families of Diptera are compiled. Functions associated with intromission and insemination (e.g. seizing and positioning the female appropriately, pushing past possible barriers within the female, orienting within the female to achieve sperm transfer), which are unlikely to be involved in new arms races when females are protected, are common (>80% of documented cases). This information is then used to generate the new arms race prediction: differences in genitalic form among congeneric species in which females are protected should be less common than differences among congeneric species in which females are vulnerable to harassment by males. This prediction was tested using a sample of 361 genera of insects and spiders. The prediction clearly failed, even when the data were adjusted to take into account several possible biases. Comparative analyses within particular taxonomic groups also failed to show the predicted trends, as did less extensive data on other non-genitalic male display traits. Arms races, as defined in some recent models, seem to have been important in male-female coevolution of genitalic structures than has been suggested. By elimination, alternative interpretations, such as traditional female choice, which do not predict associations between female protection from harassment and rapid divergent evolution, are strengthened.

6.3

WHY ARE COPULATING MALES BAD FOR FEMALES?

Kate Lessells

NIOO, Boterhoeksestraat 48, PO box 40, 6666 ZG Heteren, The Netherlands

In a number of species there is evidence that mating per se reduces the future survival of females. Because a male's reproductive success depends partially on the survival of the female with which he has just mated, such damage demands an explanation in terms of a compensating advantage to the male. One explanation is that the reduction in the female's survival is a side-effect of some other manipulation of the female. However, an alternative explanation is that damaging the female and reducing her survival is the primary target of the male's behaviour, and that the female then adaptively modifies her subsequent reproductive behaviour in a way that also benefits the male. This might occur beacuse (a) a reduction in residual reproductive value increases the female's optimal oviposition rate, and (b) an increase in the current level of damage increases the female's optimal remating interval. I will present some recent theoretical models which examine whether damaging copulation by males could indeed have evolved in this way.

Contributed talks

6.4

PATTERNS OF GENETIC CORRELATIONS BETWEEN TRAITS REQUIRED FOR MALE FERTILITY AND MANIPULATION OF FEMALE REMATING

Patricia J. Moore, V. Tamara Montrose, W. Edwin Harris, Allen J. Moore.

School of Biological Sciences, University of Manchester, Oxford, Road, Manchester M13 9PT

Sperm competition and sexual conflict have become increasingly dominant in studies of sexual selection. However, most studies investigate how sperm characteristics or sexual conflict may influence fitness and study only phenotypic variation. Here we use a quantitative genetic approach to investigate how patterns of genetic variation and covariation may ameliorate the effects of selection and influence patterns of evolution of sperm characteristics. In a half-sib study we found high levels of additive genetic variation, suggesting that evolutionary responses are possible. However, the pattern of genetic correlations suggest there may be constraints, as all sperm characteristics are strongly positively correlated except sperm viability and testes size. Despite the strong genetic correlations, most phenotypic correlations were very small and not significantly different from zero. Environmental correlations were negative, so that environmental influences had opposite effects on pairs of characters. Our studies indicate some of the pitfalls of adopting a purely phenotypic or selection approach to studying sperm competition and sexual conflict

6.5

GENETIC TRADE-OFFS IN FITNESS RELATED TRAITS IN THE FIELD CRICKET *GRYLLUS BIMACULATUS*?

Rolando Rodríguez-Muñoz, Amanda J. Bretman, Tom Tregenza

University of Leeds, School of Biology, LS2 9JT, Leeds, UK

Sexual conflict theory predicts that alleles that bring fitness benefits to one sex can be favoured by selection even if they decrease fitness when they occur in the other sex. It is possible that such effects will be transitory since there is strong selection to limit the expression of such alleles to one gender. However, there have been few attempts to examine genetic correlations between fitness related traits in both sexes. We present a quantitative genetic study using the field cricket, *Gryllus bimaculatus* where we have examined this question as well as the hypothesis that genetic trade-offs between fitness related traits could help maintain variation in such traits. Studies of potential trade-offs have typically focussed on a very small number of traits or situations where there are distinct alternative strategies. We have attempted to measure as many fitness related traits as possible in both sexes. In the wild, male field crickets shelter in holes in the ground and defend them from other males by fighting. Male calling song attracts females for mating and fertilisation is achieved by the transfer of a spermatophore. Previous research suggested the existence of trade-offs between sexually and naturally selected traits and among naturally selected traits. To investigate this possibility more rigorously, two quantitative genetics designs were performed: a full-sib design including twenty-three independent families and a full-sib half-sib design in which eleven males were each mated with three different females. Fitness related characters measured included morphological (body size), behavioural (male calling rate, fighting ability and maximum mating rate) and life history traits (hatching success, hatchling mass, developmental time, nymph survival, adult lifespan, spermatophore mass and fecundity). Correlations among traits as well as the components of phenotypic variance are estimated.

6.6

EXPERIMENTAL REMOVAL AND ELEVATION OF SEXUAL SELECTION IN A SPERM HETEROMORPHIC MODEL INSECT SYSTEM: DOES SEXUAL SELECTION GENERATE SEXUAL CONFLICT?

Helen S. Crudgington, Rhonda R Snook

University of Sheffield Western Bank Sheffield S10 2TN UK

Experimental evolution approaches have provided valuable insights into the relationship between sexual conflict and the intensity of sexual selection. Using this technique, we manipulated the opportunity for both pre- and post-copulatory sexual selection in four replicate populations of *Drosophila pseudoobscura*, a naturally promiscuous species exhibiting sperm heteromorphism. We imposed three selection regimes: a monogamy treatment in which the evolutionary interests of males and females were predicted to converge, a control promiscuity treatment that simulated natural levels of female multiple mating, and an elevated promiscuity treatment in which the opportunity and scope for sexual dissonance was expected to be greatest. We report the findings of three investigations into the fitness consequences to females mated to males with which they had or had not coevolved. Specifically, we assayed key female life-history traits including longevity, lifetime fecundity and remating interval, and examined the potential for indirect benefits to females in the form of competitive sons. We also present data from all four replicate populations on the effect of varying degrees of sexual selection on the maintenance and evolution of sperm heteromorphism.

6.7

THE EVOLUTION OF SEXUAL CONFLICT IN *DROSOPHILA MELANOGASTER*.

Stuart L. Wigby, Tracey Chapman

Dept Biology, UCL, Darwin Building, Gower Street, London, WC1E 6BT

I tested the hypothesis that alterations in the level of sexual selection and sexual conflict can lead to rapid adaptation by the sexes. To do this, adult D. *melanogaster* sex ratio was manipulated in three treatments: equal sex ratio, male-biased (3:1) or female-biased (1:3), with 3 replicates of each. The sample size was equal for all regimes, and the larval environment was standardised across all treatments. Sexual selection and sexual conflict were predicted to be most intense in the male-biased lines, intermediate in the equal sex ratio lines and least intense in the female-biased lines. After 18 generations of selection, females from each line were placed together with males from the base stock, and female longevity, fecundity, egg-fertility and mating frequency were recorded. Females from the male-biased lines lived longer than females from equal sex ratio lines, which in turn lived longer than females from female-biased lines. These longevity differences could not be explained by between-line differences in mating frequency, fecundity or egg-fertility. Instead the results suggest that these lines have diverged significantly in 'per mating' resistance to male-induced harm (the 'cost of mating'), with females from the male-biased lines being most resistant, females from the female-biased lines being least resistant and females from the equal sex lines being intermediately resistant.

6.8

ON DETECTING SEXUALLY ANTAGONISTIC COEVOLUTION WITH POPULATION CROSSES

[1]**L. Rowe,** [2]E. Cameron, T. Day

[1]*University of Toronto, Ramsay Wright Zoological Laboratories, 25 Harbord Street, Toronto, Ont, M5S 3G5, Canada*

[2]*Queen's University, Biosciences Complex, Kingston, Ont., K7L 3N6, Canada*

The results of population crosses on traits such as mating rate, oviposition rate and survivorship are increasingly used to distinguish between modes of coevolution between the sexes. Two key hypotheses, erected from a verbal theory of sexually antagonistic coevolution, have been the subject of several recent tests. First, statistical interactions arising in between population crosses are suggested to be indicative of a complex signal/receiver system. Second, under sexually antagonistic coevolution females will do "best" when mated with their own males, where best is defined by the weakest response to the signal and the highest fitness. We test these hypotheses by crossing strains generated from a formal model of sexually antagonistic coevolution. Strains differ in the strength of natural selection acting on male and female traits. In our model, we assume sexually antagonistic coevolution of a single male signal and female receptor. The female receptor is treated as a linear preference function where both the slope and intercept of the function can evolve. Our results suggest that neither prediction is consistently supported. Interactions are not diagnostic of complex signal/receiver systems, and even under sexually antagonistic coevolution females may do better mating males of strains other than their own. These results suggest a reinterpretation of several recent experiments and have important implications for developing theories of speciation when sexually antagonistic coevolution is involved.

6.9

SEXUAL CONFLICT AND REPRODUCTIVE ISOLATION IN A HYBRID ZONE

Klaus Reinhardt

University of Sheffield, Dept. Animal Plant Sciences, Sheffield S10 2TN

Reproductive isolation is the central point of speciation. Recently, it has been proposed to be largely driven by sexual conflict. Using two parapatric grasshopper populations from a hybrid zone I tested whether heterogamic matings result in a stronger harm to females than homogamic matings and compared the results to an outgroup population. Here I show that the remating interval of females is likely governed by precopulatory choice, postcopulatory choice as well postmating inhibition by male substances. The survival differences in females engaged in homogamic and heterogamic matings were consistent across all three populations. Males showed population differences in reproductive investment as well as ejaculate size allocation. Females seemed to differ in the amount of sperm stored from heterogamic and homogamic matings. This suggests that antagonistic as well as non-antagonistic processes may drive reproductive isolation.

6.10

SEXUAL CONFLICT AND SPECIATION IN RODENTS

P. Stockley

University of Liverpool, Faculty of Veterinary Science, Leahurst, Chester High Road, Neston CH64 7TE, U.K.

There is currently much interest in the idea that rapid divergence of reproductive traits associated with interlocus antagonistic coevolution may generate reproductive isolation during the speciation process. Copulatory behaviour is a conspicuous reproductive trait that has diverged dramatically among closely related mammalian taxa. In rodents, the best-studied mammalian group in this context, species-specific patterns of male copulatory stimulation trigger female physiological responses associated with pregnancy initiation and oestrus abbreviation. Antagonistic coevolution could thus generate reproductive isolation via divergence of copulatory behaviour if changes in female stimulation thresholds (or 'vaginal codes') favouring prolonged copulation are driven by post-copulatory sexual selection or conflict over remating rates. In support of this idea, a significant positive association was found between copulation duration and species richness across 25 rodent genera, although both variables also vary independently of body size and degree of polyandry (measured as relative testes size). Implications of these findings are discussed in relation to theoretical expectations concerning the role of sexual conflict in speciation

6.11

CONFLICT AND COOPERATION IN MATING SYSTEMS OF *STEGODYPHUS* SPIDERS

[1]**Alexei A. Maklakov,** [2]Y. Lubin,

[1]*Ben Gurion University, Department of Life Sciences, Beer Sheva, Israel*

[2]*Ben Gurion University, Mitrani Department of Desert, Ecology, Sede Boqer, 84990, Israel*

Polyandry may arise when 1) benefits that females accrue from multiple mating outweigh the costs or 2) males manipulate females against the females' best interests. We used a genus of web-building spiders with variable social systems to study female re-mating behaviour and the interaction between social structure and female mating. In a solitary spider *Stegodyphus lineatus* females behave aggressively towards additional males after the first mating. Female aggressiveness may act to select for better quality males (indirect selection). Alternatively females may try to avoid superfluous matings (direct selection). To test these alternatives, we allocated females into single-mating (SM) and double-mating treatments. Double-mated females either accepted (DM) or rejected (RE) the second male. DM females laid more eggs, but did not produce more offspring than SM and RE females. Offspring of DM females were smaller at dispersal than offspring of SM and RE females. Also, nest failure was significantly more common in DM females. There was no difference in adult offspring body mass between treatments. Additionally, we show that double-mating increases time to egg-laying even when females are provided with food *ad libitum*. Paternal variables did not influence female reproductive success, whereas maternal body condition explained much of the variation. Therefore, we suggest that polyandry in *S. lineatus* results from male manipulation and possible indirect fitness benefits do not outweigh the costs of re-mating. We demonstrate that *S. lineatus* females reduce their aggressiveness when costs of male cohabitation within females nest are removed. In inbred social spiders, the costs of male cohabitation are negligible while potential benefits of polyandry increase. We present comparative data on four solitary and two social species showing that sexual competition is reduced in social species and promiscuity is common.

6.12

DO INTERNALLY FERTILISING SIMULTANEOUS HERMAPHRODITES REALLY TRADE SPERM?

Nils Anthes, Nico K. Michiels,

Department of Evolutionary Biology, University of Muenster, Huefferstr. 1, 48149 Muenster, Germany

Sexual conflict theory suggests antagonistic co-evolution between the two sexes in order to maximise reproductive success (RS). Hence, selection should favour mating systems that resolve this conflict such that an increase of the own RS at the expense of the partner is minimised. The conditional alternation of sexual roles in internally fertilizing simultaneous hermaphrodites (SH), also "sperm trading", has been interpreted as a mechanism that prevents partners from mating in their preferred sexual role only ("cheating"). The lower investment in paternity suggests that generally the male role should be preferred, which is well established in gonochorists and pair-spawning SH (Bateman's principle). In internally fertilising SH, however, the situation is less clear. Based on studies in the sea slug *Navanax inermis*, it is as yet unsolved whether trading of sperm has evolved in response to a preference for the male or female role. Using more convenient, closely related species of the genus *Chelidonura*, we first tested whether sperm trading includes mechanisms that prevent cheating, thus a flexible adjustment of sperm donation to sperm reception. Contrary to conclusions from previous theoretical and non-manipulative observational studies sperm reception did not affect sperm donation suggesting that trading behaviour does not necessarily include mechanisms to prevent cheating. Secondly, we re-evaluate patterns that are suggestive of a male of female preference.

6.13

SEXUAL CONFLICT, POLYGYNY AND FEMALE MATE PREFERENCE: AVOIDANCE OF SPERM-DEPLETED MALES BY A NOVEL MECHANISM OF MATE DISCRIMINATION

W. Edwin Harris, Patricia J. Moore

University of Manchester, School of Biological Sciences, 3-614 Stopford Building, Oxford Road, Manchester, M13 9PT, UK

Females of a polygynous cockroach (*Nauphoeta cinerea*) exert a mating preference for virgin males compared to males that have mated frequently. This is likely due to sexual conflict between males and females in this species, which results from male control of female remating behavior and a reduction of female fertility following mating with males that have mated frequently previously. To investigate the mechanism of mate preference, we tested whether females discriminate among males on the basis of an intrinsic change in males due to mating, or because of some extrinsic change due to consorting with mates. In mate preference trials, we found that females were biased against males who had consorted with several females, whether he had actually mated with them or not. In a second experiment, we manipulated surface chemicals on males. In mate preference trials, we found that females were biased against males rubbed with a cotton swab applied to five females, but not males with an equivalent application derived from a single female. We propose this is a novel mechanism for mate discrimination by females, which is based on the diversity of cuticular hydrocarbons transferred to males from mates.

Posters

6.14P

SEXUAL CONFLICTS IN SOCIAL INSECTS

B. Baer, J. J. Boomsma

University of Copenhagen, Department of Population Ecology, Universitetsparken 15, 2100 Copenhagen, Denmark

Reproductive conflicts in social insects have been intensively studied both theoretically and empirically. In contrast, sexual conflicts, i.e. conflicts between males and females (queens) over paternity are poorly investigated. In particular, the little studied reproductive strategies of male social insects have a number of unique features making them interesting model systems for the study of sexual conflicts. Males hatch with a fixed amount of clonal sperm, are haploid and therefore contribute only to female offspring. The sexes have a conflict over egg fertilization since males do not transfer genes to the male offspring of their mate, which arise from unfertilised eggs. On the other hand, nasty male traits to ensure paternity at the expense of female fitness, as found in non-social insects, are probably absent in social insects. This is because insects societies are long-lived and need time to mature, which means that queen survival is essential and that large amounts of viable sperm need to be stored for the production of sterile workers before reproduction is possible. Here we present possible evolutionary outcomes of sexual conflicts in fungus growing ants. Males of some species are not only able to mate repeatedly but seem also able to transfer sperm directly to the queen's spermatheca, which is rarely found in social insects and reduces possibilities of cryptic female choice. Furthermore, males of monandrous species have small testes and large accessory glands whereas the opposite is observed in multiple mated species. This may imply that sperm competition necessitates increased investment in sperm production. Finally, we investigated sperm morphology, which might be important during sperm competition, if longer sperm swims faster and reaches the sperm storage organ earlier than shorter sperm. Contrary to our expectation, longer sperm was not associated with multiple mating of queens, but sperm length was found to be highly variable.

6.15P

ANTAGONISTIC COEVOLUTION BETWEEN MALE OFFENSE AND DEFENSE LEADS TO A HARMFUL LAG-LOAD IN FEMALES

[1]Urban Friberg, [2]Phillip G. Byrne, [3]William, R. Rice

[1]*Dept. of Animal Ecology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18d, SE - 752 36 Uppsala, Sweden*

[2]*School of Botany and Zoology, The Australian National University, Canberra ACT 0200, Australia*

[3]*Dept. of Ecology, Evolution & Marine Biology, University of California, Santa Barbara, Ca 93106, USA*

In promiscuous species males face two opposing goals. Males must prevent their own sperm from being displaced when their mates re-mate with other males (defense) and they must displace sperm resident in their mates from other males (offense). These opposing objectives of offense and defense select for high sperm displacement when a male mates a previously mated female, low sperm displacement when his mate re-mates with another male, and the ability to suppress re-mating of his mates with other males. Adaptations that facilitate these goals may harm a male's mate as an incidental byproduct. To elucidate the interrelationships between the fitness components that contribute to a male's success in fertilization, and their influence on the fitness of his mates, we tested for the presence of the relevant additive genetic variances and covariances in a population of Drosophila melanogaster. We found substantial additive genetic variation for both total defense and total offense ability. The intrinsic conflict between the observed additive genetic variance for the offense and defense of competing males provided evidence for a molecular arms-race between the genes that mediate these fitness components. We also studied the implications of this arms race on female fitness, and thus population, fitness. Genotypes that increased male offense harmed females by reducing their fecundity while those genotypes that increased male defense reduced his mate's survival but increased her fecundity.

6.16P

RAPID DIVERGENCE IN POSTMATING PREZYGOTIC TRAITS IN LAB- POPULATIONS OF *CALLOSOBRUCHUS MACULATUS*

Claudia Fricke

Department of Animal Ecology, Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden

The mechanisms of speciation are at the heart of biology and are currently much debated. Focus was earlier on processes leading to premating and postzygotic isolation, which are now relatively well understood. However, little consideration has been given to traits, which affect postmating prezygotic processes, and their effects on reproductive isolation. In this study, we measured divergence in postmating prezygotic characters, such as female reproductive rate and remating rate. We used two strains of the beetle *Callosobruchus maculatus*, each of which has been split into three different lab-populations during the last decades (i.e., a known phylogeny). Our results show that divergence between the populations occurred and that this happened very rapidly. Further, divergence occurred along different trajectories in different populations. Interactions between male-female genotypes were also found for the effects of mating on female lifespan, fecundity and early fecundity. We conclude that postmating sexual selection can lead to divergence between the populations, and hence be an important engine of speciation.

6.17P

SEXUAL COERCION VERSUS FORCEFUL COURTSHIP

[1]Susanne Plesner Jensen, [2]Elizabeth L. Bradshaw

[1]Ålshøjvej 12, 8420 Knebel, Denmark

[2]Brandish Cottage, Brandish Street, Allerford, Minehead, Somerset TA24 8HR, UK

Much has been written about sexual coercion, and evidence has been presented for its evolution due to an increased breeding success for coercive as opposed to courting males. However, we see a potential role for some use of force during courtship in species where females might gain indirect rather than direct fitness benefits from their choice of mates, and where male strength and competitive ability are traits that females would do well to select for. Forceful courtship may arise in species where females that are unable to observe these traits directly from male-male interactions, either because of low population densities or because males adopt a roaming strategy whereby females are likely to encounter males one at a time. We discuss the evolution of forceful courtship in terms of environmental conditions, breeding systems, male-male competition and physiology and suggest ways of distinguishing coercion, which is likely to have costs for the female, from forceful courtship, which may benefit females because it provides a cue to male quality

6.18P

THE EFFECT OF MALE STERILITY ON FEMALE RECEPTIVITY IN THE MEDITERRANEAN FRUIT FLY

Ken Kraaijeveld, Tracey Chapman

Department of Biology, Darwin Building, University College London, Gower Street, London WC1E 6BT, United Kingdom

Abstract Text: When females mate with more than one male, males are under selection to prevent female remating. In many insects, mating causes a reduction in female receptivity. However, the mechanisms influencing remating frequency and female receptivity are poorly understood in most species. In the present study we investigated the ability of sterilised male Mediterranean fruit flies, *Ceratitis capitata*, to obtain matings and prevent remating in females. We found that both virgin and once-mated females were less likely to mate with a sterile male than with a fertile male. Sterile males performed pheromone calling less frequently, which may explain their lower success at obtaining matings. Females that mated to a sterile male were more likely to remate than females that mated to a fertile male, especially when they were presented with a fertile second male. Sterile males transferred sperm, which suggests that other factors that may reduce female receptivity, such as the action of seminal fluid accessory gland proteins (Acps), or sperm-mediated Acp transfer were affected by the sterilisation process. Adaptations evolved in response to sexual conflict thus potentially have important implications for pest control using Sterile Insect Technique.

6.19P

SEXUAL CONFLICTS IN HERMAPHRODITES: TRADEOFF BETWEEN SEXUAL FUNCTIONS

M. C. Lorenzi, G. Sella, D. Schleicherowa, L. Ramella

University of Turin, V. Accademia Albertina 17, 10123 Torino, Italy

In contrast to gonochoric organisms, hermaphrodites sexual conflicts occur within the individual. Sex allocation theory predicts that hermaphrodites regulate female and male gamete investment to maximise their fitness on the basis of encountered conditions. However, little evidence of a tradeoff of sex allocation at the individual level has been provided. The outcrossing simultaneous hermaphrodite *Ophryotrocha diadema* appears to be an ideal model to test the outcome of hermaphrodite sexual conflicts: eggs and sperm production can be easily estimated. We tested whether individuals of O. diadema are able to trade off resources between eggs and sperm on the basis of different social conditions. Results document that individuals produced proportionally more eggs and less sperm as population density increased. At the individual level, hermaphrodites showed significantly different patterns of sex allocation as a function of the different social conditions (G-test, $G= 20.031$, $df = 8$, $P<0.02$).

6.20P

MALE SOCIAL STATUS, SPERM QUALITY, AND SEXUAL CONFLICT IN THE COCKROACH *NAUPHOETA CINEREA*

V. Tamara Montrose, Ed Harris, Allen J. Moore and Patricia J. Moore

3.614 Stopford Building, School of Biological Sciences, University of Manchester, Oxford Road, M13 9PT UK

Male social status has been shown to be associated with sperm quality. The relationship between social status and sperm quality is not consistent, however. In the domestic fowl, dominant males have sperm of lower fertilising quality, as measured by sperm motility, than subordinate males. The motility of sperm of dominant mice, however, is higher than that of subordinate mice. In addition, the sperm motility of isolated mice is higher than that of subordinate mice, suggesting that the stress of social experience may influence sperm quality. We have undertaken a study to examine the influence of male social status on sperm quality in the cockroach *Nauphoeta cinerea*. Males form dominance hierarchies and dominant males monopolise mating opportunities. Males are able to enforce female monogamy in the first reproductive bout by insertion of a spermatophore above a threshold size, and thus eliminate sperm competition in the first clutch of offspring. We have measured characteristics associated with male fertility, including spermatophore size, sperm number, sperm viability and testes size, as a function of social status. We measured spermatophore characteristics and sperm quality in naïve males, prior to social experience, and from the same males following the establishment of hierarchies, enabling us to distinguish between intrinsic characteristics correlated with social status and characteristics resulting from social experience. The relationship between sperm quality, male social status, and sexual conflict in this species will be discussed, including the effect that variation in mating system might have on the relationship between male social status and sperm characteristics.

6.21P

SEXUAL CONFLICT DURING PARENTAL CARE IN THE BURYING BEETLE *NICROPHORUS VESPILLOIDES*

Sharmin Musa, Per T Smiseth, Allen J Moore

School of Biological Sciences, 3.614 Stopford Building, University of Manchester, Oxford Road, Manchester M13 9PT, UK

Burying beetles *(Nicrophorus)* have well developed parental care, preparing a carcass and directly provisioning larvae pre-digested food. In some species burying beetle males co-operate with females in burying carrion and taking care of the offspring but male care of offspring does not enhance offspring fitness or reduce female workload. Males may stay on the carcass because parents can utilise this resource as food for themselves as well as their offspring. Therefore, there may be conflict between the parents over the use of food as offspring number and size are determined by the quantity of resources available. My experiment aimed to determine whether there was any conflict between the sexes regarding this resource utilisation and whether females could influence or control this conflict. A two-by-two experimental design was used to investigate both male condition, manipulated by starving the males for one week prior to pairing, and male size, manipulated by pairing males that were larger or smaller than their partner. Males and females gained weight during the preparation of the carcass. Starved males gained more weight than unstarved males, suggesting male condition could influence the extent of conflict. This potential conflict did not have any observed effect on either parental care or on the offspring behaviour towards their parents. A second experiment was performed that showed that weight gain occurred prior to offspring hatching and parental care, during carcass preparation. Thus, if there is sexual conflict, it occurs over foraging during the preparation of the carcass, not during parental care.

6.22P

ON THE EVOLUTION OF POLYGYNY: A THEORETICAL EXAMINATION OF THE POLYGYNY THRESHOLD MODEL

[1]Susan E. Ptak, [2]Michael Lachmann

[1]Interdisciplinary Center for Bioinformatics, Leipzig, Germany

[2]Max Planck Institute for Mathematics in the Sciences, Leipzig, Germany

The polygyny threshold model states that if costs incurred are less than the benefits gained from mating polygynously in terms of breeding-situation quality, then polygyny is favored and could evolve. We constructed mathematical models and computer simulations to evaluate this hypothesis. In the basic model, there is a single locus with two alleles, which regulates whether the female is receptive to polygyny. There are two breeding situations of differing quality on which males randomly assort. Females then select a mate based on the associated breeding situation and whether the male already has mates. This basic model is extended mathematically to include a cost for the initial female of a male with multiple mates and again to include gene expression in males. The computer simulations extend the basic model to multiple loci and alleles and to multiple breeding situations. The results presented here suggest that the polygyny threshold model is valid in a population genetic context: if the fitness of females that actually mate polygynously is greater than the fitness of monogamous females on poorer breeding situations, polygyny evolves. However, this approach reveals interesting dynamics not apparent from the verbal model. If the trait is expressed in males and females, then polygyny can evolve even if females mating polygynously have a lower fitness than females mating monogamously. In the multiple breeding-situations model, the polygyny allele increases to some equilibrium value above which it experiences no selection. Surprisingly, as the cost of polygyny increases, the equilibrium frequency of the polygyny allele also increases. The difference between this evolutionary model and the ideal free distribution is discussed.

6.23P

SEXUAL CONFLICT OVER PARENTAL CARE – DO CHICKS HAVE DOMINION?

Gavin H Thomas, T Szekely

Department of Biology and Biochemistry, University of Bath, 4 South, Claverton Down, Bath, BA2 7AY

Shorebirds and their allies (Charadrii; plovers, sandpipers, gulls and auks) display remarkable diversity in their breeding systems. Previous research has suggested that this diversity is driven by the conflict of interests of males and females. We investigate whether the diversity of shorebird breeding systems is influenced by the demands of the chicks. In contrast to parental care and social mating system, the developmental mode of shorebird young is conservative. The plovers and sandpipers are predominantly precocial - their young hatch with downy feathers and they are able to self-feed from hatching onward. The chicks of gulls, auks, and oystercatchers are semiprecocial and do not feed themselves. We use a phylogenetic comparative approach to compare rates of evolution of parental care and social mating system between precocial and semiprecocial shorebirds. Our results suggest that developmental mode has a profound influence on the diversity of breeding systems, and infer that this may affect the level of sexual conflict between parents. In shorebirds with semiprecocial offspring, both parents are constrained to provide care until fledging. In addition, they are also limited to a socially monogamous mating system. Post-zygotic sexual conflict is therefore reduced because neither parent stands to benefit from desertion. In contrast, the relaxation of constraints for care of young in precocial taxa allows a diversification of parental care and mating system. The reduced need for care in precocial taxa frees one parent to desert and heightens sexual conflict.

Symposium 7

Pleistocene refugia, colonization patterns and evolution

Organisers: Anna-Britta Berglund, Pierre Taberlet and Godfrey Hewitt

Roger Stevens Lecture Theatre 20

09.50 – 10.20	**Bennett, K.** The movement of plants in space and time
10.20 – 11.00	**Coffee**
11.00 – 11.30	**Taberlet, P.** Molecular techniques for phylogeographic studies.
11.30 – 12.00	**Crandall, K.** Analytical approaches in phylogeography
12.00 – 12.20	**Baird, S. J. E.** A novel approximation to the structured coalescent: the Dancing Trees algorithm
12.20 – 12.40	**Cooper, S. J.B.** The impact of Pleistocene environmental changes on population subdivision of species in southern Australia
12.40 – 14.00	**Lunch**
14.00 – 14.20	**Kotlik, P.** Circum Black Sea phylogeography of freshwater fish *Barbus*: divergence in the Pontic glacial refugium
14.20 – 14.40	**Babik, W.** A long leap from the East? Phylogeography of *Rana arvalis* in Eurasia
14.40 – 15.00	**Vogel, J.** Pleistocene refugia, phylogeography and polyploidy of the rockfern genus *Asplenium* in Europe: evidence from cpDNA and allozymes
15.00 – 15. 20	**Carlsson, M.** The genetic structure of North European adders (*Vipera berus*).
15.20 – 16.00 Tea	
16.00 – 16.20	**Tribsch, A.** Patterns of endemism and comparative phylogeography confirm palaeo-environmental evidence for Pleistocene refugia in the Eastern Alps
16.20 – 16.40	**Van Houdt, J. K. J.** Holarctic phylogeography of burbot (*Lota lota*): evidence for large-scale extinctions and recolonisation
16.40 – 17. 00	**Liebers, D.** The Herring Gull (*Larus argentatus*) complex is not a ring species
17.00 – 17.20	**Bronken Eidesen, P.** Effects of climate change on ecosystems in Svalbard: past and future immigration of thermophilous key species

Invited talks

7.1

THE MOVEMENT OF PLANTS IN SPACE AND TIME

Keith Bennett

Palaeobiology program, Uppsala Universitet, Geocentrum, Villavägen 16, SE-752 36 Uppsala, Sweden

The repeated glaciations in the northern hemisphere have lead to major changes in the distributions of plants. Clement Reid appreciated this more than 100 years ago and showed that even the roughest calculations suggested that taxa such as oaks must have spread into Britain at surprisingly high rates. Pollen data and radiocarbon dating have been influential in showing that trees spread into and across the northern continents individualistically: at their own times, own rates, and own directions. Rates of spread are of the order of 0.1-2 km yr-1, faster than most observed dispersal mechanisms. Communities have no long persistence in time, forming and breaking as species come and go. More detailed analysis has substantiated these views, but with modification in two directions, focussing on the apparent high rates of spread. Firstly, it appears that the significant mechanisms of spread may change depending on the time-scale of interest. Mechanisms prevalent and obvious on decadal time-scales may not be relevant on millenial time-scales, and vice-versa, complicating attempts to use observations of modern behaviour for interpretation of past behaviour. Secondly, recent discovery and documentation of macrofossil remains of trees much nearer to the maximum ice-limit (in time and space) than previously realised suggest that some rates of spread, at least, may have been over-estimated. These results have implications for the (i) using the fossil record to describe past history; (ii) interpretation of genotypic variation across modern distributions in terms of likely history (especially the location of `refugia'); and (iii) mechanisms of speciation.

7.2

MOLECULAR TECHNIQUES FOR PHYLOGEOGRAPHIC STUDIES

Pierre Taberlet

Laboratoire d'Ecologie Alpine, CNRS UMR 5553, Université Joseph Fourier, BP 53, F-38041 Grenoble Cedex 9, France

This talk gives a review of the different molecular techniques used up to now in phylogeographic studies. A few landmark studies that influenced this field are presented. The first studies, since 1979, concerned animal mitochondrial DNA and used the RFLP technique. The polymerase chain reaction (PCR) revolution, really available on the bench since 1989, completely changed the perspectives. However, it is only recently, in the last four or five years, that phylogeographic studies became very popular, about ten years after having the full technical possibilities (PCR and DNA sequencing). The molecular approaches vary greatly according to the type of genome used. DNA sequencing is the most common approach for animal mitochondrial DNA. The low variability of chloroplast DNA represents a challenge at the technical level, PCR-RFLP and non-coding region sequencing being widely used for analyzing its variability. AFLP and single-copy gene sequencing are used for assessing nuclear DNA variability.

7.3

ANALYTICAL APPROACHES IN PHYLOGEOGRAPHY

Keith Crandall

Department of Integrative Biology, Provo, Utah 84602, United States

In this talk, we describe computational approaches for estimating phylogenetic and genealogical relationships based on DNA sequence data. We discuss approaches to model selection, relative performance of different phylogenetic approaches in terms of computational speed. Finally, we describe the nested clade analysis for population genetic data analyses were reticulating relationships are typical and traditional bifurcating models of evolution are not as effective in conveying the evolutionary relationships among sequences. We will also demonstrate these methods with various examples from conservation genetic work being done in my lab.

Contibuted talks

7.4

A NOVEL APPROXIMATION TO THE STRUCTURED COALESCENT: THE DANCING TREES ALGORITHM.

S. J. E. Baird

University of California, Berkeley

The structured coalescent is often considered as a discrete space, continuous time model with waiting times between events. I describe a discrete space, discrete time approximation to the structured coalescent: trees are mapped onto a three dimensional lattice. This Dancing Trees approximation allows straightforward and efficient sampling of the properties of the structured coalescent using a composite Monte Carlo Markov chain. Comparison to existing results for unstructured and linear populations and populations on a plane show the Dancing Trees approximation is good over a wide range of constraints and scales. The algorithm in easily generalizable, allowing more complex spatial scenarios to be investigated, and allowing inference based on genetic geographic and ecological information.

7.5

THE IMPACT OF PLEISTOCENE ENVIRONMENTAL CHANGES ON POPULATION SUBDIVISION OF SPECIES IN SOUTHERN AUSTRALIA

[1]**Steven J. B. Cooper**, Agatha Labrinidis, Jan Armstrong, Kathy Saint,
Stephen C. Donnellan

South Australian Museum, North Terrace, Adelaide 5000, Australia

Pleistocene Ice Ages have led to dramatic environmental changes in Australia, cycling the landscape through periods of extreme aridity to periods considerably wetter than the present. These changes are likely to have impacted greatly on the distribution and population subdivision of species, but, to date, very few phylogeographic studies have been carried out to investigate this possibility, particularly across the broad expanse of southern and arid zone Australia. We have carried out an analysis of mitochondrial DNA (mtDNA) variation in two vertebrate species: a marsupial, the dunnart *Sminthopsis crassicaudata*, and a reptile, the sleepy lizard *Tiliqua rugosa*. Both species have widespread distributions across southern Australia, encompassing a variety of habitats in southern mesic-coastal through to arid-central regions. Phylogenetic and restriction enzyme analyses of mtDNA sequences (Control Region and ND4) identified two (dunnart) and three (sleepy lizard) major mtDNA clades that are geographically localised in each species. Each share a similar phylogeographic pattern and mtDNA divergence (3.5-4.5%) between populations in the south-east and northern regions of South Australia, suggesting that common evolutionary forces have operated to subdivide each species. The role of Pleistocene Ice ages in this process and the location of potential refugial populations (e.g., the Flinders Ranges) are discussed.

7.6

CIRCUM BLACK SEA PHYLOGEOGRAPHY OF FRESHWATER FISH, *BARBUS*: DIVERGENCE IN THE PONTIC GLACIAL REFUGIUM

[1]**Petr Kotlik**, [2]Nina G. Bogutskaya, [3]F. Guler Ekmekci

[1]*Laboratory of Fish Genetics, Institute of Animal Physiology and Genetics, Academy of Sciences of the Czech Republic, 277 21 Libechov, Czech Republic*

[2]*Zoological Institute, Russian Academy of Sciences, Universitetskaya emb. 1, 199034 St. Petersburg, Russia*

[3]*Biology Department, Faculty of Science, Hacettepe University, Beytepe Campus, 06532 Ankara, Turkey*

Phylogeography of a species complex of barbs (genus *Barbus*), which is distributed throughout the rivers all around the Black Sea, has been addressed with a mitochondrial DNA sequence marker. The aim was to assess the populations' phylogeographic response to the drastic environmental change in the Black Sea basin, which occurred after the Pleistocene-Holocene boundary when this large inland water body underwent a rapid transition from freshwater to marine conditions. Multiple phylogeographic breaks are suggestive of an allopatric divergence of regional populations, which does not support the view of the Pleistocene freshwater Black Sea lake as a universal dispersal route. A gene flow via the lake over great distance did occur within the phylogroups, however, as populations from opposite sites of the Black Sea show shallow divergence and are paraphyletic to each other. Therefore, the salinification of the Black Sea lake merely interrupted the gene flow within the phylogroups, whose origins predate this catastrophic event. Only one of the four phylogroups happened to expand throughout Europe, while the others reside within close to the Black Sea.

7.7

A LONG LEAP FROM THE EAST? PHYLOGEOGRAPHY OF *RANA ARVALIS* IN EURASIA

[1]**W. Babik** [2]W. Branicki, [3]M. Sandera, [1]J. Rafinski

[1]*Jagiellonian University, Institute of Zoology, Ingardena 6, 30-060 Krakow, Poland*

[2]*Institute of Forensic Research, Krakow, Poland*

[3]*Charles University, Faculty of Natural Sciences, Department of Zoology, Prague, Czech Rep.*

The moor frog (*Rana arvalis*) is a widely distributed Eurasian species ranging from eastern France to eastern Siberia. In Europe it is basically restricted to lowlands north of the Alps and Carpathians, a smaller semiisolated part of the distribution encompasses the Panonian Basin and Czech Rep. Present distribution indicates that the refugia of the species were not located in the Mediterranean Region. To test the hypothesis stating that Europe was colonized from Eastern European and/or Asian refugia, we studied genetic variation in a 682 bp fragment of mtDNA cytochrome b gene in 62 samples (200 individuals) covering the entire range of the species. We detected two main clades within *R. arvalis*. The clades differ in about 3.8% of nucleotide sequence. The northern clade ranges from the Netherlands to Lake Baikal and comprises 30 closely related haplotypes. This group was also found in eastern Hungary, Romania and the Czech Rep. The only distinct subclade within the northern clade, differing in about 1%, was found in southern and central Czech Rep. The southern major clade is restricted to a relatively small area in eastern and southern Austria, Slovenia and the western part of Hungary, so the Panonian basin is populated by two major groups. In the southern Czech Rep and south-western Slovakia we found populations where both haplotypes occurred. Nested Clade Analysis showed that the northern clade experienced a continuous range expansion most probably related to postglacial colonization of extensive areas of northern Eurasia. The data strongly suggest that the southern group persisted in the western part of the Panonian Basin since pre-Pleistocene times. The location of glacial refugia of the northern group cannot be determined with certainty, but most likely the vast area of northern Eurasia was recolonized from Siberian refugia.

7.8

PLEISTOCENE REFUGIA, PHYLOGEOGRAPHY AND POLYPLOIDY OF THE ROCKFERN GENUS *ASPLENIUM* IN EUROPE: EVIDENCE FROM CPDNA AND ALLOZYMES.

[1]**Johannes Vogel**, [2, 3]Harald Schneider, [4]Mary Gibby, [5]Istvan Pinter, [6]Steve Trewick, [6]Mary Morgan-Richards, [7]John Barrett, [1]Stephen Russell, [1]Sally Henderson,
[1]Fred Rumsey

[1]*Department of Botany, Natural History Museum, SW7 5BD London, UK;*

[2]*Albrecht-von-Haller Institut of Plant Sciences, University of Goettingen, 37073 Goettingen, Germany;*

[3]*Department of Biology, Duke University, NC 27708, USA;*

[4]*Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh EH3 5LR, Scotland;*

[5]*Department of Genetics, Eoetvoes Lorand University, Budapest, H-1088, Hungary;*

[6]*Department of Plant and Microbial Sciences, University of Canterbury, Christchurch, New Zealand;*

[7]*Department of Genetics, University of Cambridge, UK -*

Phylogeographic methods have provided the opportunity to elucidate the effects of large-scale historical events (such as Pleistocene climate change) on the distribution and subdivision of biota and put in context the role of reproductive biology in the genetic structuring of species. A broad spectrum of organisms have provided grist to the phylogeographic mill including animal and various plant groups, but as yet there are few published studies of fern phylogeography.

We have carried out extensive allozyme electrophoresis and cpDNA sequencing to study the discontinuities of genetic diversity, distribution and prevailing breeding systems of four European *Asplenium* polyploid complexes, comprising diploid, tetraploid and hexaploid taxa. Patterns observed in the autopolyploid *A. ceterach* and *A. trichomanes* complexes allow the inference of long-term Pleistocene refugia in the Mediterranean Basin, while the allopolyploid *A. adulterinum* complex was informative to determine Nordic refugia.

7.9

THE GENETIC STRUCTURE OF NORTH EUROPEAN ADDERS (*VIPERA BERUS*)

Martin Carlsson, Håkan Tegelström

Dept. of Conservation Biology and Genetics, Uppsala University, Norbyv. 18D, SE-75236, Sweden

Studies of post-glacial colonisation of northern Europe by terrestrial vertebrates have produced a strikingly similar pattern of bi-directional colonisation from two refugia resulting in a zone of contact in northern Sweden. Fennoscandian adders have also colonised from two glacial refugia. The two colonising lineages meet with the main contact zone being situated in the north of Finland and two more zones of contact being found in the archipelagos of the Baltic and Bothnian Seas. Here we compare mtDNA results with nuclear datasets derived from RAPD and microsatellite markers. An eastern and a western lineage are readily distinguishable using all sets of markers. The same contact zones that were derived from mitochondrial data are clearly identifiable with nuclear data. Limited gene flow occurs across the two southern zones, which have formed from of across water dispersal. Both sets of nuclear markers detect a high level of unidirectional gene flow across the zone in northern Finland, with introgression reaching far west into Sweden. When contrasted to the lack of mitochondrial introgression across the same zone, this indicates differential dispersal among sexes and lineages. Using both mtDNA sequence and microsatellite data from samples across the species' Eurasian range, the origins of the two northern European adder lineages have been traced. Both population lineages survived the last glaciation in refugia located north of the Alps, and the areas south and east thereof are populated by genetically differentiated adder populations.

7.10

PATTERNS OF ENDEMISM AND COMPARATIVE PHYLOGEOGRAPHY CONFIRM PALAEO-ENVIRONMENTAL EVIDENCE FOR PLEISTOCENE REFUGIA IN THE EASTERN ALPS

[1]**A. Tribsch**, [2]P. Schoenswetter

[1]*Department of Higher Plant Systematics and Evolution, Institute of Botany, University of Vienna, Rennweg 14, A-1030 Vienna, Austria*

[2]*Department of Chorology and Vegetation Science, Institute of Botany, University of Vienna, Rennweg 14, A-1030 Vienna, Austria*

A synthesis of palaeoclimatological and geological data, as well as distributional patterns of endemic plants and molecular phylogeographical data, can help clarify glacial refugia. Evidence is given from palaeo-environmental data that important refugia for alpine plants were situated in unglaciated areas of the Alps and also within the ice sheet on peripheral nunataks. Within the Eastern Alps, 230 taxa of vascular plants are endemic plus 49 taxa extending their distribution to the adjacent Western Alps or to the Dinaric region, and 19 taxa endemic to the forelands. The highest number of endemic species is found in limestone regions in the southern part of the Eastern Alps, which remained unglaciated. Endemic species growing on limestone, therefore, are more common that those confined to silicates (less than 15%). Intraspecific phylogeographic patterns of alpine plants obtained with AFLP fingerprinting can be interpreted in the context of refugia during the Pleistocene. Molecular data from several silicicolous alpine species (*Androsace alpina, Androsace wulfeniana, Bupleurum stellatum, Carex curvula subsp. curvula, Phyteuma globulariifolium, Ranunculus glacialis, Saponaria pumila,* and *Veronica bellidioides*) are not completely congruent, as the genetic pattern of each species was shaped not only by the ice ages, but also from biological attributes of breeding systems, dispersal abilities, etc. In most cases, however, genetic patterns can be related to glacial survival in small refugia in siliceous parts of the southern and easternmost Alps, also characterized by endemic taxa. The largest refugium for silicicolous alpine plants is in the easternmost Central Alps, where the highest number of steno-endemic species also can be found. Molecular data show, however, that large areas in the smaller southern refugia were even more important as a source for postglacial colonisation. Overall, there is good congruence between patterns of endemism, phylogeographic patterns, and refugia suggested by palaeo-environmental and geological data.

7.11

HOLARCTIC PHYLOGEOGRAPHY OF BURBOT (*LOTA LOTA*): EVIDENCE FOR LARGE-SCALE EXTINCTIONS AND RECOLONISATION

[1]**Jeroen K. J. Van Houdt,** [1]Lotje De Cleyn, [2]Alessandra Perretti,
[1]Filip A. M. Volckaert,

[1]*Laboratory of Aquatic ecology, Katholieke Universiteit Leuven, Ch. de Bériotstraat 32, B-3000 Leuven, Belgium*

[2]*University of Padova, Dipartimento di Biologia, Via Ugo Bassi 58-B, I-35121 Padova, Italy*

We analysed 256 individuals from 45 populations throughout the entire range of the burbot (*Lota lota*) (Gadidae, Teleostei) by means of mitochondrial DNA (mtDNA) sequence variation in the control region. Network analysis of the 44 observed haplotypes revealed a genetically young species, characterized by two distinct mitochondrial lineages that diverged on average by 2%. The Eurasian-Beringian lineage, observed in the Palearctic region and north of the Grate Slave Lake in North America, consisted of 30 immediately connected haplotypes that could be related to five geographic regions possibly associated with several glacial refugia. The regions at the peripheral range of this lineage were characterized by distinct derived mitochondrial variants, whereas the Euro-Siberian region was characterized by widespread central haplotypes, suggesting that transcontinental exchange of cold adapted freshwater taxa must have been possible in recent evolutionary time. The North American lineage south of the Great Slave lakes was subdivided in three mitochondrial clades, associated with known southern refugia for fish. Mitochondrial genomes that originated from glacial refugia east of the continental divide had a distribution that largely overlapped in the previously glaciated region. No exchange was observed between the southern refuge zones, but burbot probably crossed the continental divide from east to west after the last glacial maximum. Burbot might serve as a model to explore the link between historical and contemporary components of phylogeographic structuring in fish. Such global perspective on the spatial pattern of genetic variation makes comparisons among burbot at a smaller geographic scale a meaningful exercise.

7.12

THE HERRING GULL (*LARUS ARGENTATUS*) COMPLEX IS NOT A RING SPECIES

Dorit Liebers, Andreas J. Helbig

University of Greifswald, Vogelwarte Hiddensee, D-18565 Kloster, Germany

Under what circumstances speciation in sexually reproducing animals can occur without geographical disjunction is still controversial. The ring species model (Mayr 1942) suggests that a reproductive barrier may arise through 'isolation-by-distance' when peripheral populations of a species meet after expanding around some uninhabitable barrier. Based on an extensive survey of mtDNA (control region) variation we show that the classical example of a ring species, the circumpolar herring gull (*Larus argentatus*) complex, differentiated in allopatry following multiple vicariance and long-distance colonization events, not primarily through isolation-by-distance. Reproductive isolation evolved much faster between some lineages than between others, irrespective of their genetic distance. Extant taxa are the result of divergent as well as reticulate evolution between two ancestral lineages originally separated in a North Atlantic and a continental Eurasian refugium. Continental birds expanded along the entire north Eurasian coast and via Beringia into North America. Contrary to Mayr's suggestion, the circumpolar ring of interbreeding populations never closed, i.e. American herring gulls did not invade Europe. However, closure of the ring in the opposite direction may be imminent with lesser black-backed gulls

7.13

EFFECTS OF CLIMATE CHANGE ON ECOSYSTEMS IN SVALBARD: PAST AND FUTURE IMMIGRATION OF THERMOPHILOUS KEY SPECIES

[1]**Pernille Bronken Eidesen**, [1]Gro Hilde Jacobsen, [1]Inger Skrede, [2]Pierre Taberlet, [3]Kristine Westergaard, [1]Christian Brochmann

[1]*National Centre for Biosystematics, Natural History Museums and Botanical Garden, University of Oslo, PO Box 1172 Blindern, N-0318 Oslo, Norway*

[2]*Laboratoire d'Ecologie Alpine, B.P.53, 38041 GRENOBLE CEDEX 9*

[3]*Tromsø University Museum, Botany, N-9037 Tromsø, Norway*

The arctic archipelago of Svalbard was almost completely ice-covered during the last glaciation. The most thermophilous plants occurring there today must therefore have arrived postglacially by long-distance dispersal. Such species (e.g. dwarf birch and arctic blueberry) are probably relics from the hypsithermal, which was 1-2 °C warmer than today. Climate models predict an increase of the average temperature by 3-3.5 °C from 1990 to 2070 in Svalbard. Thus, even more thermophilous species may establish, given that they are able to cross the oceans. Species that dominate more southern alpine ecosystems, such as mountain birch and grey willows, will cause ecological cascade effects if they succeed to establish in Svalbard. For this recently started five-year project we have sampled 22 species in the North Atlantic region, of which 11 already are established in Svalbard and 11 are putative immigrants. We use molecular markers (mainly AFLPs), genotype assignment tests, and phylogenetic analyses to 1) identify the source areas and frequency of previous immigrations to Svalbard of the 11 established species, 2) estimate the dispersal abilities of the 11 putative immigrant species, and 3) compare the likelihood for successful immigrations of species that are bird-dispersed, wind-dispersed, and without particular adaptations. Results from five of these species will be presented.

Posters

7.14P

HOW POLLEN ANALYSIS APPLIED TO MARINE SEDIMENTS CAN CONTRIBUTE TO LOCATE REFUGIA OF THERMOPHILOUS TREES? AN EXAMPLE FROM LATE WÜRMIAN OF THE GULF OF LIONS (WESTERN MEDITERRANEAN SEA)

[1]C. Beaudouin, [1]J.-P. Suc, [2]N. Acherki, [1]L. Courtois, [3]M. Rabineau, [3]S. Berné

[1]Université Claude Bernard - Lyon 1, Laboratoire PaléoEnvironnements et PaléobioSphère (UMR CNRS 5125), 2 rue Dubois, 69622 Villeurbanne Cédex, France

[2]Université Montpellier 2, Institut de Botanique, Laboratoire de Paléoenvironnements, Archéologie et Action de l'Homme UMR 5059 CNRS, 163 rue A. Broussonnet, 34090 Montpellier (France)

[3]Laboratoire Environnements Sédimentaires, Géosciences Marines, IFREMER - Centre de Brest, BP 70, 29280 Plouzané, France

Pollen analysis, applied on continental sediments is often used (with the help of biology) to understand vegetation dynamics. From the 1970's, a lot of sites have been studied in France (more than 60 in Southeastern France). Most of them concern the last deglaciation (from 18000 BP up to the Holocene). From these data, different patterns for taxa spreading during the last deglaciation have been inferred (Brewer *et al.*, 2002 ; Ravazzi, 2002). But only 3 sites in France are able to provide an idea on the vegetation of older periods (e. g. before the last deglaciation). Their situation (northward or in the vicinity of Lyons) does not allow the reconstruction of vegetation in southern France and then are not able to evidence the presence of refugia during glacial stages. Indeed, continental sites mainly record a local vegetation which cannot be extrapolated further than some kilometres. On the contrary, marine sediments record a regional vegetation as revealed by a study made on the present-day prodelta of the Rhône river (Beaudouin *et al.*, in press). In order to study the last glacial cycle, 6 cores have been taken on the shelf of the Gulf of Lions. Several radiocarbon datings have been made. These cores provide a complete record of vegetation changes along the last climatic cycle, the beginning of the Last Glacial excepted. Pollen grains of *Picea* and *Abies* are abundant at 20000 BP whereas no pollen of these trees has been found northward Lyons. Therefore, the presence of *Picea* and *Abies* refugia in Southern France is highly suggested. This confirms Ravazzi's (2002) hypothesis based on biological data.

7.15P

ORIGIN OF THE MODERN TUNDRA ECOSYSTEM – A NEW PROJECT ON COMPARATIVE PHYLOGENETIC ANALYSIS OF SOME ARCTIC KEY GENERA

T. A. Carlsen, V. A. Albert, R. Elven, C. Brochmann

National Centre for Biosystematics, Natural History Museums and Botanical Garden, University of Oslo, P.O. Box 1172 Blindern, N-0318 Oslo, Norway

In this new project, common trends in the colonisation of plants into the arctic region in the late Tertiary - early Quaternary are investigated using comparative phylogenetic analysis based on nuclear and chloroplast DNA sequences. Widespread genera in the Northern Hemisphere that contain arctic, alpine, and boreal species have been chosen as model groups: *Tephroseris* (Asteraceae), *Smelowskia* (Brassicaceae), and section *Cardaminella* in *Cardamine* (Brassicaceae). These model groups show large variation in chromosome number, suggesting frequent polyploidisation events. Fresh material has been collected in Alaska, Canada, Europe, and Altai, and herbarium specimens from throughout the northern hemisphere will be included in the analyses. In addition to the phylogenies that will be constructed in this study, the conclusions and final analysis of the colonisation patterns will be based on phylogenies from other participants of the National Centre for Biosystematics in Norway and from other collaborating research groups.

7.16P

PHYLOGEOGRAPHY OF A GENERALIST AND A SPECIALIST PARASITOID AND THEIR COMMON HOST

J. Drögemüller, J. Johannesen

University of Mainz, Saarstrasse 21, 55099 Mainz, Germany

To understand how species co-evolve in multi-species assemblages we are investigating the level of association between a host, the tephritid fly *Urophora cardui*, and its generalist, *Eurytoma robusta*, and specialist, *E. serratulae*, parasitoids. *Urophora cardui* induces stem galls on the thistle *Cirsium arvense*. By using the different parasitoid life-histories as variables, we wish to test whether/how host-parasitoid and parasitoid/parasitoid associations interact over geographic and historical distributions. In the present investigation we study the basic population structure and phylogeography (nested clade analysis) of the three species using the mtDNA gene COI. Parasitoids were collected from *U. cardui* galls and populations holding all three species were studied. As of writing, preliminary results suggest dispersal-associations between the host and the specialist parasitoid at the historical level of dispersal, but the specialist parasitoid shows higher extant gene flow than its host. Both species have few haplotypes with star radiations, patterns of mtDNA variation typical for species experiencing recent range expansion. In contrast, the generalist parasitoid shows very high mtDNA diversity but no association between haplotype genealogies and geography. However, haplotype frequency distributions of the generalist suggest more divergence, hence less gene flow between populations, than for the specialist.

7.17P

GEOGRAPHIC STRUCTURE OF THE GENETIC DIVERSITY OF FOUR FISH SPECIES FROM CANADIAN SHIELD

M-C. Gagnon, B. Angers

University of Montreal, CP.6128, Succ. Centre-Ville, H3C 3J7 Canada

Geographic distribution of population's genetic diversity results from the influence of historical factors (post-glacial colonisation) and contemporary factors (genetic drift, migration, selection). Sympatric species with different physiological capacities may demonstrate different evolutive history. This project consists in determining phylogenetic relationships among four fish species populations (whitefish, yellow perch, walleye and northern pike) living in the same lakes of Canadian Shield. The genetic diversity of those species populations was estimated by using molecular markers located on both mitochondrial DNA and nuclear DNA in order to explore different temporal and spatial scales.

7.18P

MITOCHONDRIAL DIFFERENTIATION IN A POLYMORPHIC LAND SNAIL: EVIDENCE FOR PLEISTOCENE SURVIVAL WITHIN THE BOUNDARIES OF PERMAFROST

[1,3]M. Haase, [2]B. Misof, [1]T. Wirth, [1]H. Baminger, [1]B. Baur

[1]*Univ. Basel, St. Johanns-Vorstadt 10, 4056 Basel, Switzerland*

[2]*Museum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany*

[3]*NIWA, Hamilton, New Zealand*

The genetic differentiation of populations having colonized formerly unsuitable habitats after the Pleistocene glaciations depends to a great extent on the speed of expansion. Slow dispersers maintain their refugial diversity while fast dispersal leads to a reduction of diversity in the newly colonized areas. During the Pleistocene almost the entire current range of the land snail *Arianta arbustorum* has repeatedly been covered with ice or been subjected to permafrost. Due to the low potential for dispersal of land snails, slow (re)colonization of the wide range from southern refugia can be excluded. Alternatively, fast, passive dispersal from southern refugia or survival in and expansion from multiple refugia within the area subjected to permafrost may account for the current distribution. In order to find evidence for either of these scenarios we reconstructed a phylogeography based on the sequences of a fragment of COI from 133 individuals collected at 45 localities and analyzed the molecular variance. Seventy-five haplotypes were found which diverged on average at 7.52% of positions. This high degree of diversity suggests that *A. arbustorum* is an old species in which the population structure, isolation, and the hermaphroditic nature have reduced the probability of lineage extinction. The genetic structure was highly significant with the highest variance partition found among regions. Geographic distance and mitochondrial differentiation were not congruent. Lineages had overlapping ranges. The clear genetic differentiation and the patchy pattern of haplotype distribution suggest that colonization of formerly unsuitable habitats was mainly achieved from multiple populations from within the permafrost area.

7.19P

PLEISTOCENE RAINFOREST CONTRACTION AND MOLECULAR EVIDENCE FOR REPRODUCTIVE ISOLATION IN THE PRAYING MANTID GENUS *CIULFINA*

G. I. Holwell, M. Gillings, M. E. Herberstein

Department of Biological Sciences, Macquarie University, Sydney, NSW, Australia, 2109

Phylogeographic analyses of vertebrates in tropical rainforests of Queensland in northern Australia have provided evidence for population-level response to the contraction of these rainforests during the Pleistocene, and their subsequent re-expansion. Patterns of population-level response for invertebrates from this region have not previously been identified. The praying mantid genus *Ciulfina* is widespread throughout the wet tropics and most of Queensland. Morphological studies have found a large degree of variation in genital morphology between different populations, implying that these populations might be reproductively isolated. To test this hypothesis, we examined polymorphisms in the ribosomal RNA gene internal transcribed spacer region (ITS) of various *Ciulfina* populations. PCR was used to amplify a product containing ITS1, 5.8S rDNA and ITS2 from representative of various populations along the Queensland coast, ranging from Brisbane to Cape Tribulation. The amplified region was then digested with a panel of restriction enzymes. Considerable polymorphism was detected, allowing us to define several biogeographic regions, each containing populations with unique restriction profiles. The dynamics of the evolution of multicopy genes such as those for ribosomal RNA suggest that each unique population is reproductively isolated from all others. These data are presented in light of the known biogeographical history of the wet tropics. We are currently assessing pre- and post-zygotic mechanisms that may restrict gene flow between these populations.

7.20P

IMMIGRATION OF THE THERMOPHILOUS, BIRD-DISPERSED *EMPETRUM NIGRUM- S. LAT.* (CROWBERRY) TO SVALBARD: SOURCE AND FREQUENCY

Gro Hilde Jacobsen, Pernille Bronken Eidesen, Christian Brochmann

National Centre for Biosystematics, Natural History Museums and Botanical Garden, University of Oslo, P.O. Box 1172 Blindern, N-0318 Oslo, Norway

This study is a part of the larger project “Effects of climatic change on ecosystems in Svalbard: past and future immigration of thermophilous key species”. The principal goal of the main project is to estimate the likelihood and speed of immigration to the arctic archipelago Svalbard of plant species that dominate in more southern ecosystems, and therefore are expected to give ecological cascade effects. The aims of this subproject are to investigate the dispersal ability and to find the source and frequency of the dispersal to Svalbard for one of the species, the thermophilous and bird-dispersed iEmpetrum nigrum/i. 30 populations, each with 11 plants, were sampled from the North Atlantic region (Norway, Greenland, and Svalbard) and from two reference areas (Ural and Beringia). AFLPs (Amplified Fragment Length Polymorphisms) are used as molecular markers. Four primer combinations have been chosen after primer testing. There are two main levels of ploidy in iEmpetrum nigrum/i. The main focus in this study is on the montane subspecies iEmpetrum nigrum/i ssp. ihermaphroditum/i, which is reported as tetraploid. All samples investigated by us using flow cytometry were tetraploid, except those from Iceland, which were di- and triploid.

7.21P

COLOUR POLYMORPHISM AND GENETIC DIFFERENTIATION IN THE ARCTIC SKUA (*STERCORARIUS PARASITICUS*)

[1]Kirstin Janssen, [2]Truls Moum

[1]Dept. of Molecular Biotechnology, Inst. of Medical Biology, University of Tromsoe, N-9037 Tromsoe, Norway

[2]The Norwegian School of Veterinary Science, Kyrkjevegen 332/334, N-4325 Sandnes, Norway

The occurrence of a distinct plumage colour polymorphism in a seabird species, the Arctic skua, has provoked considerable inquiry during the past decades. The distribution of morphs (dark, pale and intermediate) is characterized by longitudinal gradients but also sudden changes within the circumpolar breeding range. Differences in feeding ecology and life history parameters between morphs have been reported. These differences could be important factors for the initiation and development of sympatric speciation processes. We are investigating the relation between genetic differentiation and plumage colour polymorphism of Arctic skua populations using several molecular genetic markers. Here, we present the population genetic structure of Arctic skuas as revealed by mitochondrial DNA sequences. The analyses are based on colour morph frequencies and mitochondrial control region sequence data from sampling sites throughout the circumpolar breeding range. Preliminary results suggest that population genetic structure correlates to both the distribution of colour morphs and geographic distance. We discuss how the moulding of genetic structure in Arctic skuas may relate to colonization patterns, ecology and incipient speciation.

7.22P

RETICULATE EVOLUTION AND SPECIES DELIMITATION IN THE ARCTIC *SAXIFRAGA RIVULARIS* (HIGHLAND SAXIFRAGE) COMPLEX

Marte Holten Jørgensen, Tove Gabrielsen, Reidar Elven, Brita Stedje,

Christian Brochmann

National Centre for Biosystematics, Natural History Museums and Botanical Garden, University of Oslo, P.O. Box 1172 Blindern, N-0318 Oslo, Norway

The delimitation of taxa in the *Saxifraga rivularis* complex is controversial. Two chromosome numbers ($2n = 26, 52$) are known, indicating a history of reticulate evolution. The complex is divided into five tentative species in the new checklist of the *Panarctic Flora* project: the circumpolar *Saxifraga hyperborea*, the amphi-Atlantic *S. rivularis*, and three Beringian taxa (*S. bracteata*, *S. flexuosa*, and *S. arctolitoralis*). The aims of the present study are to identify evolutionary lineages in the complex based on molecular data and flow cytometry, and to find morphological characters that can be used to delimitate taxonomic species. Silica dried material of three plants from each of 40 populations is investigated in addition to material of approximately 50 cultivated plants, collected in Norway, Svalbard, Jan Mayen, Iceland, Greenland, Canada, Alaska, and eastern Siberia. Herbarium material from the entire distribution area is also studied. Estimation of ploidy levels is based on flow cytometry (including previously chromosome-counted material), and molecular markers are obtained as amplified fragment length polymorphisms (AFLPs) using three primer combinations. The preliminary results suggest that approximately 150 polymorphic markers will be obtained. Morphometric analysis is performed based on characters used in floras and previous studies of the complex.

7.23P

WHERE TO GO – COMPARISON OF DISPERSAL HISTORIES OF EUROPEAN NEWTS (GENUS *TRITURUS*)

[1]Eevi Karvonen, [2]Pekka T. Rintamäki, [1]Mats Björklund

[1]Department of Animal Ecology, EBC, Uppsala University, Norbyvägen 18 D, SE-752 73 Uppsala, Sweden

[2]Department of Population Biology, EBC, Uppsala University, Norbyvägen 18 D, SE-752 73 Uppsala, Sweden

Northern European species originate from ancestors that expanded from ice-free areas, so called refugia. The number and the size of the populations surviving in refugia, and therefore the amount of genetic variation sustained in the populations can vary among species. Different kinds of footprints of Ice Ages can be distinguished. First, populations have diverged while isolated in refugia without gene flow among them during cold periods. On continental scale, population expansion from these distinct refugia during warmer periods could be seen as longitudinal lineages with secondary contact zones. However, if there were only few small populations surviving in only one refugium after several glaciation-deglaciation cycles the species might have gone through a bottleneck, i.e. lost part or most of its genetic variation. Therefore, the whole distribution area can constitute of only one lineage with little variation within it. By using mitochondrial DNA data, we have studied postglacial dispersal of European newts (Amphibia, Urodela, Salamandridae, *Triturus*). Interestingly, our data reveal different dispersal histories in these species. Relevance for speciation will be discussed.

7.24P

NORTHERN GLACIAL REFUGIA IN THE BANK VOLE (*CLETHRIONOMYS GLAREOLUS*)

[1]Petr Kotlik, [2]Jeremy B. Searle

[1]Laboratory of Fish Genetics, Institute of Animal Physiology and Genetics, Academy of Sciences of the Czech Republic, 277 21 Libechov, Czech Republic

[2]Department of Biology, University of York, PO Box 373 York YO10 5YW, UK

Traditionally temperate species are believed to have survived in 'southern' glacial refugia in Iberia, Italy and the Balkans during the last glacial maximum (20 000 years ago) when much of Europe was inhospitable to them. In 1998, Bilton et al. (Proc R Soc Lond, B265, 1219-1226) challenged this view with phylogeographic data on small mammals which suggested that some temperate species were able to survive in central and eastern Europe during the last glacial maximum and that the populations in these northern glacial refugia, rather than those in the southern Mediterranean areas, colonised much of Europe and western Siberia at end of the glaciation. Further support for such 'northern' refugia in small mammals has been provided recently from fossil remains and subsequent phylogeographic studies. The importance of non-Mediterranean refugia has also become evident from phylogeographic studies of other vertebrates such as freshwater fishes and amphibians. However, there is still much to be learnt on the precise localisation of these refugia and their impact on current species distributions. Our broad goal is to accurately position 'northern' glacial refugia in Europe and determine their role in the origin of modern temperate biota. Our model system is the bank vole (Clethrionomys glareolus) and our specific aim is to conduct a DNA phylogeographic study to localise 'northern' and all other major refugia in this species and to assess their relative significance. The bank vole has already been the subject of phylogeographic analysis, and has provided evidence for northern refugia. It occurs throughout Europe including all 3 Mediterranean peninsulae, such that the relative contribution of Mediterranean and non-Mediterranean glacial refugia to the current species distribution can be assessed. Extensive fossil deposits of bank voles allow their late Pleistocene distribution to be determined directly and provide a further genetic resource to test the phylogeographic models.

7.25P

DIRECT FOSSIL EVIDENCE ON REFUGIAL AREAS AND POPULATION MOVEMENTS IN LATE PLEISTOCENE LARGE MAMMALS OF EUROPE

[1]Adrian Lister, [2]Martin Street, [2]Elaine Turner, [1]Ian Barnes, [1]Chris Hills, [1]Tony Stuart

[1]Department of Biology, University College London, Gower Street, London WC1E 6BT, UK

[2]Forschungsbereich Altsteinzeit des Römisch Germanischen Zentralmuseums Mainz, Schloss Monrepos, 56567 Neuwied, Germany

The fossil record provides direct evidence on the past location of animal populations. With the refinement of Pleistocene stratigraphy, dating techniques, and palaeoenvironmental evidence, it is becoming possible to plot range maps for selected mammalian species through the past, and relate them to changing climate and other factors. Focussing on large mammalian herbivores across Europe, we utilise directly radiocarbon-dated specimens as the most reliable source of data. For part or all of the Last Glacial Maximum (*ca.* 22-16 ka), various large mammal species appear to be absent from northern and central latitudes of Europe. The location of their closest refugia varies: red deer (*Cervus elaphus*) in Iberia and possibly other Mediterranean peninsulae; extinct giant deer (*Megaloceros giganteus*) in the northern Black Sea area; extinct woolly mammoth (*Mammuthus primigenius*) in the western part of the central Russian Plain. The recolonisation history of these and other species after the retreat of the ice can also be plotted.

In additional to the distributional evidence, fossil morphology and DNA also provide clues to population movements. This is illustrated in relation to *Cervus elaphus*, where modern populations (subspecies) are found well outside their present ranges in the Late Pleistocene.

In this context, phylogeographic deductions based on modern mammalian DNA can be viewed as hypotheses testable by the fossil record. A 'total evidence' approach to reconstructing mammalian species histories would encompass morphology, distribution and DNA, in each case both ancient and modern.

7.26P

PHYLOGEOGRAPHY OF A CIRCUMPOLAR MARINE BIVALVE: MULTIPLE TRANSARCTIC PASSAGES AND SIGNATURES OF PLEISTOCENE ICE AGES

P. C. Luttikhuizen

University of Amsterdam, Kruislaan 318, 1098 SM, Amsterdam, The Netherlands

Arctic to temperate marine taxa of the northern hemisphere have undergone a series of range compressions and expansions during the last ice age. These events are expected to have left their signature in the spatial patterns of molecular variation in extant populations. In particular the last glacial maximum, 18,000 years ago, may have been of great influence. These hypotheses were tested in the marine bivalve *Macoma balthica*, known from fossils to be Pacific in origin, using a combination of coalescent analysis and a molecular clock calibration. Mitochondrial DNA sequence data for 295 individuals were collected from ten sites across the European distribution, and from Alaska. The Baltic Sea and Alaska share a haplotype clade that is estimated as having split off from the other haplotypes ~10-40 million years ago. This is a fascinating pattern in light of the fact that the Baltic Sea was entirely frozen during the last glacial maximum, with colonization of the area by marine flora and fauna having taken place during the last 8000 years. Multiple colonizations of the Atlantic Ocean from the Pacific by *M. balthica* may explain the strong differences found between Baltic Sea and other European populations of this species. Population divergence times for French vs. other non-Baltic European populations were estimated at a minimum of ~100,000 years ago, well before the last glacial maximum. Signatures of population divergence of *M. balthica* that appear to have originated during the Pleistocene have thus survived the last glacial maximum.

7.27P

PHYLOGENY, MIGRATION, AND EVOLUTION IN A BIPOLAR MODEL GROUP: THE GENUS *EMPETRUM* (CROWBERRY)

V. Mirré, B. Stedje, V. Albert, Ch. Brochmann

National Centre for Biosystematics, Natural History Museums and Botanical Garden, University of Oslo, P.O. Box 1172 Blindern, N-0318 Oslo, Norway

The genus *Empetrum* has a highly disjunct bipolar distribution and presents complex variation in morphology, breeding systems, fruit color and ploidy level (2x-4x). It is widely distributed in the circumpolar/boreal area of the northern hemisphere, where both red-and black/purple-fruited diploid, triploid and tetraploid plants can be found. It is much more restricted in the southern hemisphere (Chile, Argentina, Falklands Islands, Tristan da Cunha and Gough Islands), where only red-fruited diploids are found. The genus is monophyletic and shows very low DNA sequence variation, suggesting that the modern bipolar distribution results from fairly recent long-distance dispersal(s) rather than from vicarious events. The morphological characters vary significantly, and the number of species recognized is therefore highly dependent on the author. In this study, we use molecular markers to reconstruct phylogenetic relationships, to test existing hypotheses on the origin of the bipolar disjunction, and to study the evolution of breeding systems (mono- vs. dioecious), fruit colors, and tetraploidy. We also conduct morphometric analysis to clarify species delimitation for the completion of a circumpolar flora work (The Panarctic Flora, PAF). Plant material from the southern and northern hemispheres has been collected for this study. Fresh leaves and herbarium material are used to estimate ploidy levels by flow cytometry, and silica-dried material is used for testing AFLP (amplified fragment length polymorphism) variation based on four primer combinations.

7.28P

HISTORY OF PONTO-CASPIAN CRUSTACEAN SPECIES FLOCKS INFERRED FROM RIBOSOMAL (18S, 16S) DNA SEQUENCE

Nikolai Mugue, Olga Zueva

N.K.Koltzov Institute of Developmental Biology RAS, 26 Vavilov St. Moscow, 117808, Russia

Caspian Sea is the largest salt lake in the World, and it is harboring number of endemic species flocks, including amphipods family *Gammaridae* (over 60 species) and *Corophiidae* (7 closely related species), as well as few other crustacean groups. Analysis of 18s RNA partial sequence reveals large cluster of recently diverged species from genera *Pontogammarus, Niphargoides, Dikerogammarus,* and *Pandorites,* which present the most recent explosion of speciation in this region. Genera *Gmelina, Stenogammarus,* and *Amathillina* have slightly deeper roots with longer history of speciation in this basin. Molecular phylogenetics supports marine origin of modern Ponto-Caspian fauna. This group is very distant from Lake Baikal amphipods, as well as from *Gammarus fossarum, G. pulex,* and *G. lacustris* species groups. Despite long paleogeographic history of Ponto-Caspian biota, most of the amphipod species have relatively recent origin, which may be attributed to the dramatic fluctuations in salinity of this basin followed by mass extinction. Degree of genetic divergence in *Corophium* group is close to *Dikkerogammarus-Pontogamarus-Niphargogammarus* species flock, which may indicate that speciation took place at the same period. In addition to the Caspian Sea, Volga and Ural river deltas, Ponto-Caspian amphipods inhabit now brackish waters of several large river estuaries of Black Sea basin, with populations isolated by Mediterranean-like fauna of the Black Sea. 16sRNA sequence of specimens from different estuaries shows that these populations accumulate genetic distance which may possible result in speciation event on the secondary contact. Recent findings of cryptic *Dikerogammarus* species in European rivers may be result of independent invasions from different rivers (i.e. Danube and Dnestr) populations.

7.29P

COMPARATIVE PHYLOGEOGRAPHY OF *APODEMUS SYLVATICUS* (RODENTIA, MURIDAE) AND ONE OF ITS DIRECT AND SPECIFIC ENDOPARASITE, *HELIGMOSOMOIDES POLYGYRUS* (NEMATODA, HELIGMOSOMOIDEA), IN THE WESTERN PALEARCTIC REGION.

[1,2]C. Nieberding, [3]S. Morand, [1]R. Libois, [1,2]J. Michaux

[1] *Unité de Recherches Zoogéographiques, Institut de Zoologie, Quai van Beneden, 22, 4020 Liège, Belgium*

[2] *Laboratoire de Paléontologie-cc064, Institut des Sciences de l'Evolution de Montpellier (UMR 5554-CNRS), UM2, Place E. Bataillon, 34095 Montpellier cedex 05, France.*

[3] *Centre de Biologie et de Gestion des Populations, Campus international Agropolis de Baillarguet CS 30016, 34988 Montferrier-sur-Lez cedex France*

This study establishes for the first time the complete phylogeographic patterns of two wild European species biologically linked by a « host-parasite » association : the field mouse *Apodemus sylvaticus* (Muridae) and one of its direct and specific endoparasites, the Nematode *Heligmosomoides polygyrus* (Heligmosomoidea). The mitochondrial cytochrome b gene was sequenced in 110 specimens of both species. The results reveal a complete spatial congruence of phylogeographic patterns. Both species are split into three major genetic lineages: the western European, the Italian and the Sicilian ones, which are separated by high levels of sequence divergence. The woodmouse and its parasite recolonised western and northern Europe at the end of the Pleistocene from an Iberian refuge. Within the western European lineage, the parasite is characterized by a gradual decrease of genetic divergence from South-western Europe to the North confirming a southern refuge for this species. The genetic variability observed in both species is mainly distributed among the three major lineages, suggesting that the same historical events are responsible of that genetic structure in both the parasite and its host. A temporal congruence of their phylogeographic patterns is therefore likely. This model seems therefore powerful to compare the evolution of phylogenetically distant species over the same time period : this is the ideal situation to understand global evolutionary processes such as genes' molecular evolution absolute rate.

7.30P

GENETIC AND BIOGEOGRAPHIC HISTORY AND POPULATION STRUCTURE OF THREE FOREST SPECIES OF THE *ANOPHELES DIRUS* COMPLEX OF MOSQUITOES IN SOUTHEAST ASIA

[1]Samantha M. O'Loughlin, [2]Pradya Somboon, [3]Hirohisa Kishino,
[3]Hitome Nagamune, [1]Catherine Walton

[1]School of Biological Sciences, University of Manchester, Manchester, M13 9PT, UK

[2]Department of Parasitology, Faculty of Medicine, Chiang Mai University, Chiang Mai, Thailand

[3]Graduate School of Agriculture and Life Sciences, University of Tokyo, Tokyo, Japan

Relatively little is known about the effects of climatic variation on the flora and fauna of Southeast Asia. Studies of Amazonia and Queensland suggest that the extent of forests would have been severely reduced during the ice ages with the potential for confining forest species to fragmented refugia. The members of the *Anopheles dirus* complex of closely related mosquito species are important vectors of malaria in Southeast Asia and they occur only in forests. *An. dirus* A and D have widespread distributions with a narrow zone of overlap along the Thai-Myanmar border. *An. dirus* C appears to be associated with rocky limestone outcrops that occur in the central region of the Thai-Myanmar border extending southwards into peninsular Thailand. Previous studies of the mitochondrial DNA locus cytochrome oxidase I and microsatellites in species A and D have found patterns of genetic variation indicative of a recent population expansion. It has been hypothesised that species A and D were confined to a single area of Pleistocene rainforest refugia which acted as a source for a later demographic range expansion. By contrast, two species C populations showed no evidence of population expansion and exhibited a high level of differentiation. In this study the number of mosquito individuals was increased to more than two hundred and the number of sampling locations was also increased. A further mtDNA locus, cytochrome oxidase II, was sequenced for all individuals. The data was analysed to make inferences of population history and gene flow regimes in all the species and to test the hypothesis of range expansion in species A and D, identifying potential source populations as likely refugia. A wide range of statistical methods were used including nested clade analysis and a maximum likelihood method to make joint estimates of population sizes and migration rates.

7.31P

RAPID EVOLUTION OF MIGRATORY STRATEGIES IN A PASSERINE BIRD SHOWN BY MTDNA SEQUENCE ANALYSIS

[1]Javier Pérez-Tris, [1]Staffan Bensch, [2]José Luis Tellería, [2]Roberto Carbonell

[1]*Lund University, Department of Animal Ecology, Ecology Building, 22362 Lund, Sweden*

[2]*Universidad Complutense de Madrid. Departamento de Biología Animal I. Facultad de Biología. 28040 Madrid*

Different migratory strategies require complex orientation mechanisms, morphological adaptations and life-history adjustments. From an evolutionary perspective, it is decisive to know how fast this complex combination of traits can evolve. We studied mitochondrial control-region sequence variation in 71 blackcaps *Sylvia atricapilla* with different migratory behaviours. At a reduced geographic scale, we studied migratory and sedentary populations in Spain, which differ in clutch size, survival and flight-related morphology. We also analysed migratory individuals from Sweden, which are located on the other side of a migratory divide in Europe and perform the longest migrations known in the species, and sedentary blackcaps from the Canary Islands, which are isolated by distance from the other populations. These latter populations were chosen as representing the two extremes in terms of variation in migratory behaviour and isolation in blackcaps. Our results show that differences in migratory behaviour are not correlated with variation in a rapidly evolving neutral genetic marker. Between-population differences explained around 9% of molecular variance, but no significant part of this variation could be attributed to differences between migrants and residents (despite their great morphological and behavioural differences), suggesting a rapid divergence of migratory strategies in blackcaps. In fact, mismatch-distribution analyses suggested a rapid expansion of migratory blackcaps after a population bottleneck, probably occurred in Pleistocene refugia, while residents would not have experienced such strong population-size changes. These results show that complex combinations of behavioural, morphological and life-history traits like the ones forming migratory strategies can evolve in a relatively short term, supporting the idea that even the most divergent migration patterns may rapidly adjust to historical environmental changes.

7.32P

PHYLOGEOGRAPHY OF A TERRESTRIAL SLUG SPECIES COMPLEX IN EUROPE: TO WHAT EXTENT CAN PLEISTOCENE GLACIATIONS EXPLAIN THE OBSERVED GENETIC STRUCTURE?

[1]J. Pinceel, [1]K. Jordaens, [1]S. Geenen, [1]N. Van Houtte, [2]T. Backeljau

[1]*University of Antwerp, Department of Biology, Evolutionary Biology Group, Groenenborgerlaan 171, B-2020 Antwerp, Belgium*

[2]*Royal Belgian Institute of Natural Sciences, Vautierstraat 29, B-1000 Brussels, Belgium*

Arion subfuscus (Draparnaud) is a common and widespread native European terrestrial slug which has been introduced into several other continents. The species is regarded as a complex of several cryptic taxa. Approximately 2000 specimens from 200 locations across its native distribution range were investigated using allozymes (nine loci), mtDNA (16S rRNA) and nDNA (ITS1). All markers consistently revealed three cryptic taxa. A first taxon was restricted to Western Europe, a second, most widespread, occurred in Central and Eastern Europe and a third was restricted to the easternmost parts of Eastern Europe. Within the West European taxon, three strongly diverged lineages (23, 11 and 23% mtDNA sequence divergence) were detected. Based on nDNA and allozymes however, these lineages were found to hybridise where they co-occurred. The geographic patterns observed in our data showed that: i) haplotype and nucleotide diversities were very low in the northern parts of Europe, suggesting that single haplotypes colonized vast areas, ii) recently expanded haplotypes have restricted distribution ranges suggesting that current gene flow is slow and iii) in Southern Europe, where glacial refugia are expected, slugs were restricted to mountainous areas. Haplotype diversities of populations in the Massif Centrale, the Alps, the Balkans and the Carpathians were comparable to those of northern populations. Nucleotide diversities however were much higher. Phylogeographic inferences in relation to the observed patterns will be discussed and compared with current findings on colonisation capacity and ecology of slugs.

7.33P

IMMIGRATION OF THE HARDY, WIND-DISPERSED *DRYAS OCTOPETALA* (MOUNTAIN AVENS) TO SVALBARD: SOURCE AND FREQUENCY

[1]Inger Skrede, [2]Inger Nordal, [1]Pernille B. Eidesen, [1]Christian Brochmann

[1]National Centre for Biosystematics, Natural History Museums and Botanical Garden, University of Oslo, P.O. Box 1172 Blindern, N-0318 Oslo, Norway

[2]Division of Botany and Plant Physiology, Department of Biology, University of Oslo, P.O. Box 1045 Blindern, N-0316 Oslo, Norway

This project is part of the larger project "Effects of climate change on ecosystems in Svalbard: past and future immigration of thermophilous key species". The principal objective of this larger project is to estimate the likelihood and speed of immigration to the arctic archipelago Svalbard of plant species that dominate in more southern ecosystems and therefore are expected to give ecological cascade effects. In this particular subproject, we focus on one more hardy species, *Dryas octopetala*, and investigate its dispersal ability in the North Atlantic region and the source and frequency of its dispersal to Svalbard. Material has been collected from several northern Atlantic areas (Norway, Svalbard, Greenland and Iceland), and some reference populations were collected from other areas (Alaska and The Urals). A total of 250 plants from 24 populations is currently analysed for Amplified Fragment Length Polymorphisms (AFLPs). 35 primer combinations have been tested, and four of these combinations were selected for full analysis. Each primer combination results in ~30 polymorphic markers

7.34P

CRYPTIC NORTHERN REFUGIA AND THE ORIGINS OF THE MODERN BIOTA

John R. Stewart

AHRB Centre for the Evolutionary Analysis of Cultural Behaviour in the Institute of Archaeology, University College London

Increasingly, recent developments in both palaeontology and phylogeography are causing certain workers to question the dominant views of where refugial areas for temperate organisms were located during the most recent (and presumably previous) cold episode(s). This debate had previously been restricted to one between palynologists, on the one hand, and plant-macro and mammalian palaeontologists on the other. The former believing that southern areas such as, in Europe, the peninsulas of Iberia, Italy and the Balkans were the sole refugia during glacials. The latter, meanwhile, finding evidence for more northerly-located refuges in the form of the charcoal of temperate trees and the bones of woodland mammals. The comparatively new science of phylogeography is generating evidence for both points of view and so debate continues. However, the fact phylogeography has found any evidence of northern refugia indicates that the absolutely dated fossils of, for instance, 13 kyr BP Oak charcoal in the Belgian Ardennes were not mistakenly interpreted.

7.35P

TRACING A SOIL ARTHROPOD: POST GLACIAL COLONIZATION OF THE EUROPEAN CONTINENT

M .J. T. N. Timmermans, J. Mariën, S. C. Verhoef, J. Ellers, N. M. Van Straalen

Vrije Universiteit, De Boelelaan 1085, 1083 HV Amsterdam, The Netherlands

The genetic structure of a species is influenced by its history as well as by current gene flow. The Quaternary glaciation periods in Europe have had a major impact on the distribution of many species. During cold periods many organisms were restricted to warmer refugia in the sourthern part of Europe. Species distributions observed today are hypothesized to result from recolonizations northward. If this hypothesis is valid, populations from the southern part of Europe should genetically be more diverse compared to populations from the northern part of Europe. We tested this hypothesis using the springtail species *Orchesella cincta*. Fifteen locations throughout Europe were sampled. To obtain estimates of genetic variation AFLP markers were used. To gain information on intraspecific phylogeographic variation and past colonization routes mtDNA sequences and differences in a nuclear encoded gene were taken into account. Results based on mtDNA sequences suggest the species is divided into three different groups, with low variation in the north-western part of Europe. Our aim was to determine whether these differences are caused by past colonization, genetic drift or natural selection.

7.36P

PHYLOGEOGRAPHY OF ATLANTIC SALMON (*SALMO SALAR*) FROM NORTHERN EUROPE

[1]A. Tonteri, [2]A. Veselov, [3]S. Titov, [4]J. Lumme, [1]C. R. Primmer

[1]*University of Helsinki, Department of Ecology and Systematics, Division of Population Biology, P.O. Box 65, FIN-00014 University of Helsinki, Finland*

[2]*Institute of Biology, Karelian Research Center, Pushkinskaya 11, 185610 Petrozavodsk, Russia*

[3]*State Research Institute on Lake and River Fisheries, Makarova 26, 199053 St. Petersburg, Russia*

[4]*University of Oulu, Department of Biology, P.O. Box 3000, FIN-90014 University of Oulu, Finland*

Despite being intensively studied, the origin of North European Atlantic salmon (*Salmo salar*) has remained unclear. An eastern ice-lake refugium has been suggested as the origin of Northwest Russian salmon and a more southern refugium as the origin of the salmon in lakes Ladoga and Onega and in the Baltic Sea. In both areas an Atlantic influence has also been suggested. Here, 17 microsatellite loci were used as genetic markers to study the population genetic structure of 24 Atlantic salmon populations from northern Europe, including 18 populations from Northwest Russia. On average, the eight non-anadromous (landlocked) populations displayed significantly lower levels of genetic diversity and higher levels of inter-population divergence than the anadromous populations. This is probably due to the absence of gene flow and the presumably small effective population size of the non-anadromous populations. Individual assignment efficiency was high, both at the regional level and at the population level, indicating that the populations have retained their genetic identity and have not been drastically affected by the introduction of non-indigenous individuals. Construction of a neighbour-joining phylogenetic tree and principal component analysis revealed four groups corresponding very well to the sampling regions. >From the results of this study it is suggested that an eastern ice-lake refugium contributed to the post-glacial colonisation of Atlantic salmon to the areas of White and Barents Sea and to some, but not all, landlocked populations.

7.37P

THE CONSENSUS OF GLACIAL REFUGIA IN EUROPE RECONSIDERED

[1]M. Vila, [2]A. Ödeen

[1]*Department of Animal Ecology, EBC, Uppsala University, Norbyvägen 18D SE-752 36 Uppsala, Sweden*

[2]*Department of Biological Sciences, Simon Fraser University, Burnaby, BC, V5A 1S6 Canada*

The idea that most of the European biota would have been unable to survive glacial periods *in situ* and had to seek for refuge in Southern Europe and North Africa during the cold Pleistocene stages originated in the 19th century. The current consensus, however, is that European biota survived the glacial maxima and were genetically differentiated in three geographically isolated refugia: Balkans, Italy and Iberia. Accordingly, very few biogeographic studies encompass a significant sampling from North Africa or the Middle East. We argue that modern biogoegraphy commonly neglects the fact that Europe is not a biogeographic zone, but constitutes the northern part of the Western Palaeartic. Many authors acknowledge the straits of Gibraltar and Sicily-Tunisia as barriers for most terrestrial fauna after the Late Miocene. Others do reckon connections over both during the Pleistocene glacial maxima. Geological evidence is ambiguous, for the eustatic changes are often overprinted by tectonic movements, e.g. in the Sicilian area. The -120 m isobate usually assumed to reconstruct coastlines during the late glacial maximum has been reset to –140 m and there is evidence that it could have been deeper in former, stronger glacial maxima. We reviewed the limited evidence collected from North Africa and the Middle East to investigate whether these regions have been wrongfully dismissed as Pleistocene refugial areas. Genetic results and fossil evidence agree with a North African refugium in birds (*Motacilla*), lizards (*Podarcis hispanica*), mammals (*Apodemus sylvaticus*), insects (*Apis mellifera*). Surveys of marine molluscs and fish show significant differentiation between the Atlantic and West and East Mediterranean populations. However, findings are not conclusive. We considered whether a North African refugial area, having linked populations in Southern Europe, would entail a revision of the allopatric explanation to why many Palaearctic species form patchworks of distinct geographic variants.

7.38P

PHYLOGEOGRAPHY AND POSTGLACIAL HISTORY OF SOME IBERIAN POPULATIONS OF THE BUTTERFLY *EREBIA TRIARIA* (NYMPHALIDAE: SATYRINAE): TRACKING DIFFERENT ISOLATION EVENTS

[1,2]Marta Vila, [2]J. Ramón Vidal-Romaní, [1]Mats Björklund

[1]Department of Animal Ecology, EBC, Uppsala University, Norbyvägen 18D SE-752 36 Uppsala, Sweden

[2]IUX-Faculty of Sciences, University of A Coruna, Campus da Zapateira s/n E-15071 A Coruna, Galicia, Spain

The butterfly *Erebia triaria* is currently found above 700 m in some mountain ranges in the northern half of the Iberian Peninsula and the Alps. To test for significant differences among geographical locations, we sequenced 361 bp of the mitochondrial control region and 786 bp of the cytochrome-oxidase-I in 105 specimens from six Iberian populations (five from the NW Iberian Peninsula, and one in the Pyrenees, n = 12-20 each). Two additional geographically separated populations were also included in the analyses (Central Spain, n = 5 and Alps, n = 16). The NW populations are assumed to be currently isolated from each other since the last deglaciation, after been merged in the lowlands during cold periods (glacial maxima).

Fifty-one haplotypes were obtained. All populations resulted in significantly high F_{st} values. We found that the northwestern most Iberian population was the genetically most differentiated (average paiwise $F_{st} = 0.81$). Moreover, it showed higher phylogenetic affinity to the Portuguese and Central Spain populations than to the geographically closer ones. The maximum likelihood estimates for migration rates indicated that this northernmost population does not exchange individuals with any other. The star-like haplotype network for the northernmost population suggested a demographic expansion and, in fact, there was evidence for recent bottlenecks and expansions, after surveys based on coalescence theory performed on the NW Iberian populations.

We interpreted such a phylogeographic pattern as caused by a former isolation event, highly likely a prior glacial maximum.

A comparison of the pattern found with the one shown by a sympatric congeneric species in the NW Iberia may shed some light in the distinction between ancient and recent events affecting genetic variation.

7.39P

PHYLOGEOGRAPHY OF THE HARDY ARCTIC PLANT SPECIES *SAXIFRAGA RIVULARIS* : SOURCE AND FREQUENCY OF IMMIGRATION TO SVALBARD

[1]Kristine Westergaard, [1]Inger G. Alsos, [3]Arve Elvebakk, [2]Christian Brochmann

[1]Tromsø University Museum, Botany, N-9037 Tromsø, Norway

[2]National Centre for Biosystematics, Natural History Museums and Botanical Garden, University of Oslo, P.O. Box 1172 Blindern, N-0318 Oslo, Norway

[3]Institute of Biology, University of Tromsø, N- 9037 Tromsø, Norway

This Master project is part of the larger project "Effects of climate change on ecosystems in Svalbard: past and future immigration of thermophilous key species". The aim of the main project is to estimate the likelihood of immigration of ecological key species from more southern areas to Svalbard following climate change. A few hardy species such as *Saxifraga rivularis* are also included in the main project, because such species can more easily establish after dispersal and thus provide more reliable statistics on the frequency of immigration to Svalbard. In this subproject, I use AFLP (Amplified Fragment Length Polymorphism) data to study the geographic pattern of the molecular variation within *Saxifraga rivularis* in Svalbard, as well as in possible source areas in the North Atlantic region. The species is widespread in Svalbard, growing in late snowbeds and along small streams. It has no mechanisms for long-distance dispersal, and reproduces by seeds and runners. Plant material was collected in Svalbard, Jan Mayen, Iceland, Greenland, Northern and Southern Norway, thus covering the total distribution area. In each area, up to 11 individuals were collected from each of one to five populations. Preliminary results will be presented.

Symposium 8

Are transmission modes important for the evolution of mutualistic symbioses?

Organisers: Duur K. Aanen & Jacobus J. (Koos) Boomsma

Conference Auditorium 2

09.50 – 10.20	**Frank, S, A.** Host control of symbiont transmission: the separation of symbionts into germ and soma
10.20 – 11.00	**Coffee**
11.00 – 11.30	**Herre, E. A.** Do general laws govern mutualisms? Abstractions and realities
11.30 – 12.00	**Lutzoni, F.** What can we learn from lichens about the origin, maintenance and deterioration of mutualism?
12.00 – 12.20	**Wenseleers, T.** Conflict and cooperation in symbiotic systems: prospects for synthesis
12.20 – 12.40	**Nash, D. R.** Transmission, dispersal and evolution of trophobiotic symbionts of ants
12.40 – 14.00	**Lunch**
14.00 – 14.20	**Aanen, D. K.** Fungus-growing social insects and symbiont transmission modes
14.20 – 14.40	**Poulsen, M.** Incompatibility mechanisms of fungus clones cultivated by Acromyrmex leaf-cutting ants
14.40 – 15.00	**Korb, J.** Transmission modes of fungal symbionts in fungus-growing termites (Macrotermitinae) and their implications
15.00 – 15. 20	**Belliure, B.** Does Tomato Spotted Wilt Virus benefit its vector *Frankliniella occidentalis*?
15.20 – 16.00	**Tea**
16.00 – 16.20	**Bédhomme, S.** Resource availability and parasite virulence in *Aedes aegypti* infected with a microsporidia
16.20 – 16.40	**Capelle, J.** Virulence and mode of transmission in wild populations: a plant/parasite study case
16.40 – 17. 00	**Gil, R.** The minimum gene set to sustain endosymbiotic life: comparative analysis of reduced genomes

Invited talks

8.1

HOST CONTROL OF SYMBIONT TRANSMISSION: THE SEPARATION OF SYMBIONTS INTO GERM AND SOMA

Steven A. Frank

Dept. Ecology & Evolutionary Biology, University of California, Irvine, CA 92697-2525 USA

Obligate, vertically transmitted symbionts occur in many species. Hosts often have elaborate developmental processes and specialized organs to control the reproduction and transmission of their symbionts. In insects, control mechanisms sometimes divide the symbionts into reproductive, germline lineages and nonreproductive, somatic lineages. This germ-soma distinction favors reduced competition among symbionts, leading to a higher unit of selection in which host and symbiont reproductive interests coincide. Observations suggest a repeated evolutionary trend toward host control of symbionts and division of symbionts into germ and soma. Theory predicts that host control evolves only in response to particular mechanisms of symbiont competition, for example, when symbionts disrupt host development.

8.2

DO GENERAL LAWS GOVERN MUTUALISMS? ABSTRACTIONS AND REALITIES.

Edward Allen Herre

Smithsonian Tropical Research Institute, Unit 9408, APO AA 34002-9408, USA

Models of the evolution and stability of mutualistic systems are inspired by our understanding of their natural histories. Similarly, our understanding of their natural histories are often viewed through the lens of our models. I will discuss the implications of recent empirical findings on three diverse tropical mutualisms (figs and their pollinator wasps; host plants and their mycorrhizal fungi; and host plants and their foliar endophytic fungi) for different approaches to modelling the stability of mutualisms. One of the obvious conclusions is that it is difficult to produce relevant theory if the fundamentals of the natural history are misunderstood.

8.3

WHAT CAN WE LEARN FROM LICHENS ABOUT THE ORIGIN, MAINTENANCE AND DETERIORATION OF MUTUALISM?

Francois Lutzoni

Department of Biology, Duke University, Durham, NC 27708-0338 USA

It could be argued that for mutualism to be maintained, natural selection should increase the benefits and reduce the costs for each partner. However, it is also expected that natural selection would favour individuals that benefit most from interacting with their partner while minimizing the costs of being part of this symbiotic interaction. The latter evolutionary process is likely to shift symbiotic interactions from mutualism to a one-way exploitation. What are the factors leading to the origin, the maintenance and the deterioration of mutualism? The lichen symbiosis seems to be one of the most stable mutualistic systems. Comparative studies on closely related omphalinoid mushroom species, where mutualism recently evolved, in conjunction with the reconstruction of lichenization and delichenization across the Ascomycota phylum, where the origin of lichens is old, shed new light on evolutionary mechanisms that are potentially at work during gain, maintenance and loss of mutualism. A synthesis of these studies on lichen symbioses and their implications on our understanding of the evolution of mutualistic systems in general, will be presented.

Contributed talks

8.4

CONFLICT AND COOPERATION IN SYMBIOTIC SYSTEMS: PROSPECTS FOR SYNTHESIS

Tom Wenseleers, Francis L.W. Ratnieks

University of Sheffield, Dept. of Animal and Plant Sciences, Western Bank, Sheffield S10 2TN, UK

The evolution of intraspecific cooperation, being guided by fundamental laws such as Hamilton's rule, is now well understood and easy to make predictions about. Regarding interspecies symbioses however, a general synthesis has yet to emerge. Here we will present a conceptual overview of some symbioses, from the yucca moth and fig wasps associations, to the fungus-leafcutter ant mutualism, and make a formal comparison to ideas drawn from the intraspecific cooperation and conflict literature. For example, which types of conflicts can arise in symbioses and how is conflict resolved? What is the role of coreplication and codispersal in setting the degree of conflict? And does coreplication perhaps have a role similar to kinship and correlated interaction in intraspecific cooperation?

8.5

TRANSMISSION, DISPERSAL AND EVOLUTION OF TROPHOBIOTIC SYMBIONTS OF ANTS

David R. Nash

Department of Population Ecology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen East, Denmark

Many ant species have symbiotic interactions with homopterans and lycaenid butterflies, primarily based on trophobiosis, and covering the entire range from facultative mutualism to.parasitism. The host ant colony in such interactions is usually large, long-lived and sedentary compared to the trophobionts with which it interacts. The dispersal strategy of symbionts will thus determine whether subsequent generations are more likely to interact with the same host colony (within-host transmission) or other host colonies (horizontal transmission). The reproductive and dispersal strategy of the host colony will also influence the transmission mode of trophobionts, with budding allowing vertical transmission while independent colony foundation is more likely to promote horizontal transmission. In addition, the infection of host ant colonies by trophobionts is likely to depend on their social structure, since thresholds for recognition of "self" and "non-self" are expected to vary with such features as queen mating frequency, number of queens and colony size. In this presentation I will review the association between the nature of trophobiotic interactions (mutualistic or parasitic; facultative or specific) and the dispersal strategies and social structure of both hosts and trophobionts

8.6

FUNGUS-GROWING SOCIAL INSECTS AND SYMBIONT TRANSMISSION MODES

Duur K. Aanen, Jacobus J. Boomsma

Department of Population Ecology, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen Denmark

Two groups of social insects have independently evolved an obligate ectosymbiosis with two unrelated groups of basidiomycete fungi, viz. the macrotermitine termites and the attine ants. In spite of these completely independent origins, these agricultural symbioses have a number of remarkable "convergent" similarities: The symbiosis has allowed both the insects and the fungi to occupy previously inaccessible niches and the extent of specificity of the insect-fungus interactions is similar in spite of fundamentally different modes of transmission (Aanen et al., 2002). Theory predicts that hosts and symbionts in asymmetrical symbioses are in conflict over symbiont transmission (Frank, 1996). Selection favours symbionts to disperse out of the vertical host lineage. The ensuing decrease in relatedness between symbionts within a single host then favours within-host competition among symbiont strains and the evolution and/or expression of virulent traits. Hosts are therefore expected to evolve traits that reduce mixing of their symbionts. Fungus-growing termites generally acquire their fungi from the environment (horizontal transmission) whereas fungus-growing ants obtain their fungal symbiont from the parent colony of the nest-founding queen (uniparental vertical transmission). In line with this, fungus-fruiting is common in fungus-growing termites and extremely rare in ants. All presently available data indicate that nests of fungus growing ants and termites never have more than a single strain of fungal symbiont. This is particularly remarkable in the termite case and suggests active and continuous interference by the hosts to prevent multiple symbionts to get established.

8.7

INCOMPATIBILITY MECHANISMS OF FUNGUS CLONES CULTIVATED BY *ACROMYRMEX* LEAF-CUTTING ANTS

Michael Poulsen, **Jacobus J. Boomsma**

University of Copenhagen, Zoological Institute, 2100 Copenhagen, Denmark

Mutualistic fungi of leaf-cutting ants are ancient vertically transmitted clones. However, extant populations have considerable genetic variation of fungal clones across colonies of the same ant species and sympatric *Acromyrmex* species tend to share a number of these clones. This indicates that unintended horizontal transmission is occurring at some frequency. Previous work (Bot, Rehner & Boomsma, Evolution 2001) has suggested that ancestral (free-living) incompatibility reactions between these fungal strains have been maintained to help resident fungus gardens to eliminate such occasional horizontal infections and that the tending ants are also highly effective in recognising and eliminating fragments of alien fungus. We are now able to provide evidence that these mycelial incompatibility mechanisms do indeed exist when fungal strains are reared on artificial medium and that the intensity of incompatibility is proportional to the (AFLP) genetic distance between fungus clones. We have also obtained evidence that the incompatibility substances hitchhike through the ant gut to be expressed in the faecal droplets of ants when these are applied to fertilize a fragment of alien fungus. These results closely match predictions of host-symbiont conflict theory over the mixing of symbionts (Frank, 1996) and indicate that symbiont switching in leaf-cutting ants is highly constrained.

8.8

TRANSMISSION MODES OF FUNGAL SYMBIONTS IN FUNGUS-GROWING TERMITES (MACROTERMITINAE) AND THEIR IMPLICATIONS

[1]**Judith Korb**, [2]Duur K. Aanen

[1]*University of Regensburg, Biologie I, Universitaetsstr, 93040 Regensburg, Germany*

[2]*University of Copenhagen, Department of Population Ecology, Zoological Institute, Universitetsparken 15, 2100 Copenhagen, Denmark*

Mutualistic associations between different organisms are theoretically expected when the interests of independently reproducing units are aligned to form a single reproductive unit. However, host and symbionts can be in conflict over the transmission of the symbiont with hosts favouring uniparental, vertical transmission while symbionts will be selected to disperse independently of the host (Frank, 1996). Similar to fungus-growing ants (Attini), fungus-growing termites (Macrotermitinae) live in an obligate symbiosis with fungi (in termites: Termitomyces) on which they depend for nourishment. In contrast to the ants where uniparental transmission of the fungus occurs by default, most termite-fungus associations have horizontal transmission which probably represents the ancestral state. However, in two unrelated apical Macrotermitinae genera uniparental, vertical transmission has evolved where only one sex of the two primary reproductives carries sexual spores from the parental fungus comb to inoculate the new fungus comb (Johnson et al., 1981; Aanen et al., 2002; Korb and Aanen 2003). Remarkably, symbiont transmission is exclusively paternal in *Macrotermes bellicosus*, while symbionts are maternally inherited in all *Microtermes* species studied so far. In accordance with the different transmission patterns, the life cycle of the fungus differs between the two groups of termites with fungal fruiting being very common in most species, while being absent in associations with uniparental, vertical transmission. This might imply that in these associations the termites have won the conflict over transmission by inhibiting the development of fruiting bodies. Further implications of the transmission mode (a) on the degree of mutualism and (b) about a potential influence of the fungal symbiont on the sex ratio of the termite colony will be discussed.

8.9

DOES TOMATO SPOTTED WILT VIRUS BENEFIT ITS VECTOR *FRANKLINIELLA OCCIDENTALIS*?

[1]**Belén Belliure**, [1]Arne Janssen, [2]Paul Maris, [1]Maurice W. Sabelis

[1]*Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94084, 1090 GB Amsterdam, The Netherlands*

[2]*Laboratory of Virology, Wageningen University, Binnenhaven 11, 6709 PD Wageningen, The Netherlands*

Frankliniella occidentalis, the main vector of Tomato Spotted Wilt Virus, has been reported to colonize and oviposit preferentially on TSWV-infected plants compared to virus-free plants. To test whether this preference is related to host plant quality and/or to the performance of viruliferous thrips larvae, the effect of TSWV-infection in both host plant and vector was studied. Survival, developmental time and body growth of *Frankliniella occidentalis* larvae was compared on clean, thrips damaged, and TSWV-infected pepper plants. Thrips larvae on pepper plants that were mechanically infected with TSWV had significantly higher survival, shorter developmental time and faster body growth than thrips larvae on uninfected or damage-free plants. TSWV-infected larvae in general grew faster, whereas thrips-damaged pepper plants allowed for lower thrips survival. Implications of our results for the vulnerability of thrips with respect to its natural enemies are discussed, as well as the possible effect of the virus on the induced response of the plant to herbivores.

8.10

RESOURCE AVAILABILITY AND PARASITE VIRULENCE IN *AEDES AEGYPTI* INFECTED WITH A MICROSPORIDIA

Stéphanie Bédhomme, P. Agnew, C. Sidobre, Y. Michalakis

Centre d'Etudes sur le Polymorphisme des Microorganismes UMR 9926 IRD, 911 avenue Agropolis, BP 64501 34394 Montpellier Cedex 5 France

Host-parasite interactions imply competition for food resources between the host and the parasite growing in it. Moreover, the consumption of a part of the host resources by the parasite is one of the causes of virulence, *i.e.* the fitness cost imposed on the host by the parasite. We tested the influence of the host's nutritional conditions on the virulence of the parasite in the experimental system composed of the mosquito *Aedes aegytpi* and the microsporidium *Vavraia culicis*. .We found a condition-dependent expression of virulence and established a link between virulence and transmissibility in this system. We also investigated how the fitness of each of the partner of the interaction varies through a nutritional gradient and demonstrate that host fitness and parasite fitness are not always negatively correlated. The sign of the correlation depends on the amount of nutritional resources available to the host.

8.11

VIRULENCE AND MODE OF TRANSMISSION IN WILD POPULATIONS: A PLANT/PARASITE STUDY CASE

Julien Capelle, Claire Neema

INAPG, 16 rue Claude Bernard, 75231 PARIS Cedex 05

Theoretical models predict that virulence depends on parameters such as mode of transmission or occurrence of co-infection. Here we present preliminary data of a host plant/fungal parasite patho-system in wild populations. We investigated two populations in the area of origin of the wild bean, *Phaseolus vulgaris/Colletotrichum lindemuthianum*. AFLP genotyping of 86 strains collected from infected plants show that inter-plant migration is likewise very rare. Moreover, co-infection is frequently observed in the plants. We also suggest that saprophytic phase might be important in the evolution of the parasite, indeed, mechanisms occurring in the soil or during long distance migrations might provide other key parameters influencing the evolution of *C. lindemuthianum/P. vulgaris*.

8.12

THE MINIMUM GENE SET TO SUSTAIN ENDOSYMBIOTIC LIFE: COMPARATIVE ANALYSIS OF REDUCED GENOMES

[1]**Rosario Gil**, [1]Francisco J. Silva, [2]François Delmotte, [1]Fernando González-Candelas, [1]Amparo Latorre, [1]Andrés Moya

[1]*Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Universitat de Valencia, Polígono La Coma s/n, 46980 Paterna (Valencia), Spain*

[2]*Institut National de la Recherche Agronomique, Unité Mixte de Recherche en Santé Végétale. Domaine de la Grande Ferrade, 33883 Villenave d'Ornon Cedex, France*

Comparative analyses of the small size genomes of symbiotic and parasitic bacteria provide interesting insights into the evolution of resident genomes and the minimum set of genes necessary for intracellular life. We performed a comparative analysis of the five known genomes from insect endosymbiotic bacteria (*Wigglesworthia glossinidia*, *Blochmannia floridanus* and three strains of *Buchnera aphidicola*). Our study reveals that they share only 316 genes, a number that may be close to the minimum gene set necessary to sustain endosymbiotic life. Interestingly, in all these genomes about 27% of the genes are devoted to information storage and processing, and most of these genes are shared by all of them. Our findings also suggest that the molecular mechanisms necessary for survival in an intracellular environment may be quite similar for any endosymbiotic association, since about a third of the coding capacity of each endosymbiont seems to be dedicated to specific requirements of the respective symbiosis, mainly reflecting differences in host lifestyle, nutritional needs, and location within the host cells. When the complete set of protein-coding genes shared by all five sequenced endosymbionts genomes was compared with the genome of the intracellular parasite *Mycoplasma genitalium*, only 181 putative homologous genes were found. These genes that are present in all resident genomes analyzed may represent the basic subset of genes required for intracellular life, while the rest of the genes shared by all five endosymbionts but absent in *M. genitalium* can be considered as essential for endosymbiotic functions.

Posters

8.13P

THE ROLE OF DIFFERENT FUNGI IN TERMITE FUNGUS GARDENS

[1]Vera I. D. Ros, [2]Duur K. Aanen, [1]Alfons J. M. Debets, [3]Thomas Læssøe

[1]*Laboratory of Genetics, Wageningen University, Arboretumlaan 4, 6703 BD Wageningen, Netherlands*

[2]*Department of Population Ecology, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen, Denmark*

[3]*Department of Mycology, Botanical Institute, Øster Farimagsgade 2D, DK-1353 Copenhagen K, Denmark*

The mutualism between fungus-growing insects (beetles, ants, termites) and their fungi has become a model system in the study of symbiosis. Termites of the subfamily Macrotermitinae are known to have an obligate mutualistic relationship with basidiomycete fungi of the genus *Termitomyces*. This relationship has been well studied. *Termitomyces* has not been found growing outside termite nests and is therefore believed to be an obligate symbiont, growing as a dominant culture in the fungus comb, which is built and maintained by the termites. When the comb is removed from the nest however, it is rapidly covered by a dense growth of hyphae of other fungi, predominantly the ascomycete *Xylaria*. Several studies have mentioned the appearance of *Xylaria* when the combs are dead or removed from the nest, but the role of this fungus is still not clear. As no *Xylaria* structures are found in active nests, its growth or at least it's fruiting seems to be suppressed. In this study, the role of *Xylaria* is investigated. 55 nests of fungus-growing termites (belonging to four genera) were sampled in South-Africa. After incubation, *Xylaria* appeared on 67% of the combs, for the termite genus *Odontotermes* even on 91% of the combs. More specific analyses (using DNA techniques) are currently performed to determine (I) what the distribution of *Xylaria* in Macrotermitinae is, (II) what the exact role of *Xylaria* is in the symbiosis (parasitic, mutualistic), (III) if the *Xylaria* species found in the nests also occur outside termite-nests, (IV) if there is any specificity of *Xylaria* for different termite or *Termitomyces* species.

Symposium 9

Genetic biodiversity in natural populations: implications for management

Organisers: Kerstin Johannesson, Armando Caballero and Jesús Fernández

Conference Auditorium 1

09.50 – 10.20	**Hedrick, P.** Effective population size in endangered species
10.20 – 11.00	**Coffee**
11.00 – 11.30	**Bernatchez, L.** Challenges in assessing genetic biodiversity: an empirical illustration through recent research on salmonid fishes
11.30 – 12.00	**Via, S.** The genetics of ecological speciation on a geographic scale
12.00 – 12.20	**Hollander, J.** Evolution of reproductive barriers
12.20 – 12.40	**Leblois, R.,** Maximum likelihood inference of demographic parameters from microsatellites data : precision and robustness of a new algorithm
12.40 – 14.00	**Lunch**
14.00 – 14.20	**Bakker, J.** Genetic differentiation in experimental *Drosophila melanogaster* metapopulations
14.20 – 14.40	**Wang, J.** Estimating admixture proportions from genetic data
14.40 – 15.00	**Griebeler, E. M.** Spatial genetic patterns generated by admixing populations of two cryptic species
15.00 – 15. 20	**Carvajal-Rodríguez, A.** Effect of contamination processes on intra- and interpopulation genetic diversity
15.20 – 16.00	**Tea**
16.00 – 16.20	**van der Linde, K.** Genetic differences on a local scale
16.20 – 16.40	**Ernande, B.** Adaptive changes in harvested populations: Plasticity and evolution of age and size at maturation
16.40 – 17. 00	**Jehle, R.** The spatio-temporal genetic structure of subdivided newt populations
17.00 – 17.20	**Zhang, X.-S.** Response of genetic variation to a bottleneck in population size

Invited talks

9.1

EFFECTIVE POPULATION SIZE IN ENDANGERED SPECIES

Phil Hedrick

Department of Biology, Arizona State University, Tempe, AZ 85287, USA

Neutral molecular variants are now widely used for various conservation applications. The estimation of evolutionary parameters in endangered species from molecular data is of both general scientific interest and conservation use. An important evolution and conservation parameter is the effective population size, both in the past and in the present. Here I will show how molecular data and population genetics theory can be used to estimate the effective population size in endangered species. The examples illustrating these approaches are (1) the estimation of the long-term effective population size in three large, endangered fishes of the lower Colorado River, (2) the estimation of the size and duration of the genetic bottleneck in the Florida panther and (3) the estimation of effective population size, and the Ne/N ratio, in returning winter run Chinook salmon. These examples illustrate some of the potential uses of genetic markers and population genetics theory to understand the effective population size in evolutionary time, in recent generations, and the current generation.

9.2

CHALLENGES IN ASSESSING GENETIC BIODIVERSITY: AN EMPIRICAL ILLUSTRATION THROUGH RECENT RESEARCH ON SALMONID FISHES.

L. Bernatchez

Biologie, Université Laval, Quebec, Canada

Conservation geneticists are still facing many challenges in terms of assessing genetic biodiversity and inferring its relevance for management of natural populations. First, we still have to agree on the most appropriate method to delineate relevant patterns of population structuring for conservation purposes. In particular, the weak correlation that has been reported between diversity at neutral markers and that at quantitative traits has raised concerns regarding the usefulness of neutral markers for conservation. This also stressed the need for documenting genetic structure at genes that can be more informative in terms of adaptation. While this can be accomplished by various methods, conceptual and practical limitations are still restraining our ability to routinely apply them in most contexts. A second and related important aspect that has been debated concerns the geographic scale of genetic structuring that should be considered for management. This is not an easy issue since most species are genetically structured in a hierarchical manner, implying various levels of connectivity through gene flow. Thirdly, given the accelerating pace of demographic and environmental changes to which organisms are exposed, it is also becoming urgent for bioconservation to elucidate the evolutionary processes responsible for shaping adaptative genetic diversity. Using recent empirical studies on salmonid fishes, I will illustrate how conservation efforts can be better deserved by; i) integrating both neutral and potentially selected traits in studies of population structure and ii) considering the significance of population structuring at various geographic scales. Finally, I will show how recent empirical research on salmonid fishes is also contributing to the understanding of processes that may be driving the maintenance of adaptive genetic diversity.

9.3

THE GENETICS OF ECOLOGICAL SPECIATION ON A GEOGRAPHIC SCALE

Sara Via

University of Maryland

The process of speciation is likely to be messy. Not only does it not occur all at once, but it doesn't necessarily occur at the same rate over the entire range of the involved taxa. Populations of a pair of diverging taxa across geographical space may be at different points in the process of divergence due to variation in local selection, isolation by distance and the local occurrence of adaptive mutations. Determining why some populations may be closer to speciation than others may reveal much about the speciation process. Pea aphids on alfalfa and red clover in New York and Iowa USA) are highly ecologically specialized incipient species. However, pea aphids in western North America vary in their degree of ecological specialization on alfalfa and red clover. I will discuss the geographical variation that we have found in host use and reproductive isolation, in order to address fundamental issues about how ecological specialization and reproductive isolation evolve on a continental scale.

Contributed talks

9.4

EVOLUTION OF REPRODUCTIVE BARRIERS

Johan Hollander, Kerstin Johannesson

Tjärnö Marine biology Laboratory, SE-452 96 Strömstad, Sweden

When in a polymorphic lineage, speciation occurs due to similar mechanisms in different places because of similar selection pressure, this is taken as evidence of ecological rather than stochastic factors promoting reproductive isolation. *Littorina saxatilis* displays a strong polymorphism and subpopulations of contrasting morphology live in the same shores but in different microhabitats. Along the Swedish West Coast two ecotypes with different appearances live in adjacent sites of contrasting habitats. Differences in shape, size and habitat are features that might influence the genetic exchange between ecotypes. To investigate if the ecotypes are reproductively isolated, we performed mate choice tests in the laboratory to reveal if ecological separation might be enough to create reproductive barriers even between genetically very close populations of the same species. We stretched the analyse to investigate if size differences between the ecotypes owing to dissimilar selection pressure where the main mechanism to sustain assortative mating. The survey showed that the strong disruptive selection pressure had a significant input to specialization and deviation of the ecotypes. This specialization shapes the snails into different size classes and contributes to create a reproductive barrier.

9.5

MAXIMUM LIKELIHOOD INFERENCE OF DEMOGRAPHIC PARAMETERS FROM MICROSATELLITES DATA : PRECISION AND ROBUSTNESS OF A NEW ALGORITHM.

[1]**Raphael Leblois,** [2]Maria De Iorio, [3]François Rousset, [1]Arnaud Estoup, [2]Bob Griffiths

[1]Laboratoire Modélisation et Biologie Evolutive, CBGP-INRA, 34988 Montferrier sur Lez, France

[2]Department of Statistics, University of Oxford, 1 south Park Road, Oxford, OX13TG, UK

[3]Laboratoire Génétique et Environnement, CNRS-UMR 5554, 34095 Montpellier, France

Numerous methods have been designed to estimate migration rates and/or population sizes from genetic data. Maximum likelihood methods are supposed to be more efficient than classical methods based on summary statistics such as FST. A new method of inference has been adapted from De Iorio and Griffiths (manuscript) to take into account the stepwise nature of microsatellite mutation process in a two population model. In order to test the precision and the robustness of this method to mutational and sampling factors, we used an exact generation by generation algorithm. This extremely flexible algorithm produces individual genotypes that have evolved under various demographic models. Emphasis will be on the robustness of the estimation to: (i) deviations from the strict stepwise model of mutation, (ii) small sample sizes (number of individuals and loci genotyped) and (ii) the existence of other populations around the two populations sampled. Finally, future developments of this type of methods will be discussed.

9.6

GENETIC DIFFERENTIATION IN EXPERIMENTAL *DROSOPHILA MELANOGASTER* METAPOPULATIONS

Joke Bakker, Franjo Weissing, Kuke Bijlsma

University of Groningen, P.O.Box 14, 9750 AA Haren, Netherlands

Nowadays, many species exist in small, fragmented populations where gene flow through migration is restricted, and local extinction and recolonization are frequent events. The patterns of genetic variation in such metapopulations and the consequences for population persistence are poorly understood. We study how the interaction of genetic and demographic factors affect the ultimate genetic structure by systematically comparing results from experimental metapopulations with predictions derived from individual-based simulation models. We used *Drosophila melanogaster* metapopulations with different migration regimes and without migration. Each setup was replicated at least three times, and we monitored allele frequencies over 20 generations or more. The results are mostly in line with standard theory qualitatively, but not quantitatively. These deviations between experimental results and standard theory are most likely caused by the *Drosophila* mating system, the stepping stone migration pattern and the timing of migration. Standard population genetic models assume random fusion of gametes and migration from a migrant pool with an equal migration rate *m* between infinitely many demes, while in our experiments *Drosophila* has a polygynous mating system, and migration follows a unidirectional stepping stone pattern. Simulations taking these factors into account are in much better agreement with experimental results than the predictions based on standard theory. A third important factor is the moment of migration, that may also cause large deviations from standard theory. We conclude that even in our simple *Drosophila* model system we find systematic deviations from standard theory, indicating that details such as mating system and migration pattern are very important. Preliminary results indicate even larger effects in our current experiments that include local extinction and recolonization. Thus, extreme caution is required when standard theory is applied to natural systems, which are much more complex than standardized experiments.

9.7

ESTIMATING ADMIXTURE PROPORTIONS FROM GENETIC DATA

Jinliang Wang

Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK

For an admixed population, an important question is how much genetic contribution is from each parental population. Several methods have been developed to estimate such admixture proportions using data on genetic markers sampled from parental and admixed populations. I propose a likelihood method to estimate jointly the admixture proportions, the genetic drift occurred to the admixed population and each parental population during the period between the hybridization and sampling events, and the genetic drift in each ancestral population within the interval between their split and hybridization. The results from extensive simulations using various combinations of relevant parameter values show that in general much more accurate and precise estimates of admixture proportions are obtained from the likelihood method than previous methods. The likelihood method also yields reasonable estimates of genetic drift occurred to each population, which translate into relative effective sizes (N_e) or absolute average N_es if the time when the relevant events (such as population split, admixture, sampling) occurred is known. The proposed likelihood method also has features such as relatively low computational requirement compared with previous ones, flexibility for admixture models and marker types. In particular, it allows for missing data from a contributing parental population. The method is applied to a human data set and a wolf-like canids data set, and the results obtained are discussed in comparison with those from other estimators and from the previous studies.

9.8

SPATIAL GENETIC PATTERNS GENERATED BY ADMIXING POPULATIONS OF TWO CRYPTIC SPECIES

[1]E. M Griebeler, [2]J. C Müller, [1]A. Seitz,

[1]University of Mainz, Institute of Zoology, Department of Ecology, D-55099 Mainz, Germany

[2]GSF - National Research Center for Environment and Health, Institute of Human Genetics,
Ingolstaedter Landstrasse 1, D-85764 Neuherberg, Germany

Invasions of alien species constitute a growing threat to biodiversity. Especially, invasions of cryptic species, taxa that are morphological identical but genetically distinct, are often not perceived or are misinterpreted. Unfortunately, spatial patterns of genetic variation that are generated during the invasion process of such species are not clearly identified. Detecting general effects on genetics of admixing populations would help to identify and to assess range expansion of populations of cryptic species. To study changes in the genetic structure of populations during the invasion process, we developed an individual based simulation model for admixture of genetically distinct populations. Our model considers a linear array of demes. Migration between demes follows a one-dimensional stepping stone model. Each deme is assigned a capacity of N individuals and migration between two neighbouring demes occurs with a constant rate m. Two neutral loci represent the genetic system in a diploid organism. At the beginning of admixture half of the demes located at one edge were inhabited by identical populations of cryptic species A and the others by species B, respectively. All demes were populated at capacity N. After each generation simulated, samples were randomly drawn from each deme. Several values assumed for Nm were studied. For different periods of admixture, we performed several genetic analyses based on the random samples obtained from each deme. We calculated (1) allele frequencies, (2) linkage disequilibria, (3) deviations from Hardy-Weinberg expectations of loci, (4) pairwise genetic similarities (Slatkin's M^), and (5) assignment probabilities of individuals. We will present spatial genetic patterns that occurred during admixture of populations and will assess the statistical power of genetic measures used to detect an ongoing invasion process. The results presented herein may be applied to cryptic species inhabiting serial habitats like rivers or coast lines.

9.9

EFFECT OF CONTAMINATION PROCESSES ON INTRA- AND INTERPOPULATION GENETIC DIVERSITY

A. Carvajal-Rodríguez, E. Rolán-Alvarez, **A. Caballero**

Departamento de Bioquímica, Genética e Inmunología. Facultad de Ciencias. Universidad de Vigo. 36200 Vigo (Spain)

Computer simulations were carried out to assess the impact of different types of contamination effects on genetic diversity in natural populations. Distinct scenarios were addressed including local adaptation by natural stabilising selection, environmental stochasticity and variable migration rates. The contaminated population is assumed to be part of metapopulation setting, and contamination effects were simulated in five different ways: (1) change in the fitness optimum of the population, (2) reduction in the reproductive rate of the individuals, (3) increase in the environmental variance, (4) increase in the population isolation, and (5) decrease in the carrying capacity. The study was made in terms of intra- and interpopulation genetic variability both at neutral and quantitative genetic variation. We show that only a drastic reduction in reproductive rate has a main impact on intrapopulation variability. Quantitative interpopulation variation is generally more sensitive than neutral one to contamination effects, particularly those producing fragmentation of the metapopulation, the particular distribution of adaptive peaks being of fundamental importance.

9.10

GENETIC DIFFERENCES ON A LOCAL SCALE.

Kim van der Linde, Paul M. Brakefield, Jan G. Sevenster, Jacques J. M. van Alphen, Bas J. Zwaan,

Leiden University, Kaiserstraat 63, 2311 GP Leiden, The Netherlands

The impact of human activity on the natural environment is visible almost everywhere. Sometimes, these differences are clear and the negative impact for the biodiversity is evident. After a clear-cut of the rainforest, only some well-adapted pioneer species can survive. For that reason, less invasive logging methods have been developed. Recent studies have showed that sometimes species diversity could even increase in such areas as forest-edge species establish themselves in the selectively logged areas. However, a simultaneous loss of genetic diversity could still occur as the invading population has to adapt to the changed environment, and genetic variation have been reduced because the population went through a bottleneck. Changes in genetic variation could occur even when the new environment is within the normal range of habitats occupied by a species. Habitat related adaptation in life-history traits in *Drosophila* is almost exclusively studied in the laboratory often with flies collected over latitudinal clines, sometimes as long as a whole continent. The impact of habitat changes on populations on relative short distance of a few kilometres is rarely studied, and field studies are even rarer. In 1998, we carried out two field experiments in Panama to measure habitat-related differences in three life-history traits: development time, starvation resistance, and body size. We established two short transects of a few kilometres with each three habitats: closed canopy forest, grassland with scrub patches and an intermediate transition zone. This range in habitats is naturally occupied by most species in our study. The results show that populations, from adjacent collection sites but from different habitats, differ genetically and that different species follow the same pattern. The consequences of these results for the management of genetic diversity will be discussed.

9.11

ADAPTIVE CHANGES IN HARVESTED POPULATIONS: PLASTICITY AND EVOLUTION OF AGE AND SIZE AT MATURATION

[1]**Bruno Ernande**, [1]Ulf Dieckmann, [3]Mikko Heino

[1]*Adaptive Dynamics Network, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria*

[2]*Institute of Marine Research, P.O. Box 1870 Nordnes, N-5817 Bergen, Norway*

Concern has recently grown about potentially harvest-induced adaptive changes in the life history of exploited populations. One important issue when dealing with such adaptive changes is to distinguish between evolutionary and plastic responses because of their different management implications. Mitigating adverse evolutionary changes takes generations whereas phenotypically plastic responses occur within generations. Phenotypic plasticity can be depicted by reaction norms, which themselves are genetically determined. Therefore, to disentangle the two types of response, one can assess evolutionary changes in life history traits by modifications in their reaction norm. Statistical studies on field data showed such evolutionary changes in some exploited fish stocks, for instance. However, in order to understand underlying causes and to evaluate alternative management practices, past selective pressures must be quantified and predictions of future evolutionary changes are needed. In this respect, modelling the ecological and evolutionary dynamics of harvested populations is a critical challenge. In this paper, we model the evolution of reaction norms for age and size at maturation due to harvesting. We show that harvesting induces evolutionary changes in the position and the shape of the reaction norm for age and size at maturation. These changes qualitatively differ according to the life stage harvested. The sensitivity of the evolutionary response depends on the maturity state of harvested individuals, the type of harvesting, and the precise life history characteristics of the species considered. Evolutionary changes in the maturation reaction norm have strong repercussions on the mean size and the density of harvested individuals that, in most cases, result in reduction of biomass, a consequence that population dynamical models would overlook. These results highlight the importance of considering evolutionary trends in the long-term management of exploited living resources and give qualitative insights on how to minimize detrimental consequences of harvest-induced evolutionary changes in the maturation reaction norm.

9.12

THE SPATIO-TEMPORAL GENETIC STRUCTURE OF SUBDIVIDED NEWT POPULATIONS

[1]**R. Jehle**, [2]J. W. Arntzen, [1]T. Burke,

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

[2]*National Museum of Natural History, P. O. Box 9517, 2300 RA Leiden, The Netherlands*

The common observation of uneven spatial distributions of individuals is central for the population genetics theory. It also forms the basis of the metapopulation concept that is widely used for conservation and management purposes. However, the consequences of metapopulation dynamic processes for the maintenance of within-species genetic diversity are incompletely understood, and theoretical predictions are rarely complemented with empirical data. We quantified the amount of genetic drift and dispersal in subdivided populations of pond-breeding newts (*Triturus cristatus, T. marmoratus*), using maximum likelihood and bayesian assignment methods. The study site is situated in an agricultural landscape in western France. It encompasses 20 ponds inhabited by both species and spaced at geographical distances roughly matching maximum individual dispersal over one generation (~1 km). Approximately 2000 individuals were genotyped over eight (*T. cristatus*) and five (*T. marmoratus*) microsatellite loci. Probably in connection with a recent invasion of the study area, eight out of 16 analysed *T. cristatus* subpopulations showed a significant excess of heterozygotes, indicating past genetic bottlenecks. Conversely, all *T. marmoratus* subpopulations appeared in mutation-drift equilibrium. Measures of genetic drift, obtained through temporal samples collected at intervals of up to four generations, reveal effective subpopulation sizes of 9-19% of the actual census sizes; immigration also seems to have contributed to the observed changes in allele frequencies. Assuming a dispersal profile negatively exponentially related to geographic distance, the relative number of migrants from larger to smaller populations is significantly higher than vice versa. The contemporary effective metapopulation sizes (not considering extinction-recolonisation processes) are mainly influenced by the variance in subpopulation size and subpopulation connectivity. The results predict a substantial genetic erosion of pond-breeding amphibians in situations typical for temperate landscapes.

9.13

RESPONSE OF GENETIC VARIATION TO A BOTTLENECK IN POPULATION SIZE

Xu-Sheng Zhang, William G. Hill,

University Of Edinburgh, Institute Of Cell, Animal And Population Biology, West Mains Road, Edinburgh, EH9 3JT, UK

Recently, a comprehensive model of genetic variation under stabilizing selection was advanced, in which individuals undergo real stabilizing selection due to mutational effect on the quantitative trait of interest as well as direct selection due to pleiotropic deleterious effect on fitness. Dominance coefficients of mutational effect decrease with increasing size of mutational effects and mutations for fitness are more recessive than for the trait. With typical estimates of most relevant mutation and selection parameters and assuming infinite population, this mutation-selection balance model can provide a satisfactory explanation for the observed levels of the genetic variance under strong stabilizing selection in natural populations (Zhang and Hill 2002, Zhang et al 2003). As the population size shrinks, (partially) recessive deleterious mutations are more likely to become homozygous, which will further incur changes in other genetic properties such as mean performance, variance of fitness and variances of quantitative traits. We take advantage of this model to investigate how genetic properties of a population respond to sudden change in its effective size and how this inform the management of conserved populations.

Posters

9.14P

POPULATION GENETICS OF ZEBRA MUSSEL (*DREISSENA POLYMORPHA*, PALLAS), AN EXOTIC BIVALVE MOLLUSC RECENTLY INTRODUCED IN IRELAND

I. Astanei, E. Gosling,

Galway-Mayo Institute of Technology, Dublin Road, Galway, Ireland

Dreissena polymorpha is an invasive species that is indigenous to the Caspian Sea, but is widespread throughout most of northern Europe and eastern North America. The mussel was accidentally introduced into Ireland in 1994, and has since spread throughout its major river and lake systems. The source population(s) of Irish zebra mussels is at present unknown. Genetic diversity was analysed at 3 microsatellite loci in five Irish and one UK population. In addition, variation was analysed in the Irish populations using eight polymorphic protein markers. Irish populations exhibit similar levels of heterozygosity at both allozyme (0.37-0.45) and microsatellite loci (0.33-0.47) to those reported for European and North American populations, indicating that the number of individuals in the Irish founder population(s) was not small. Pairwise comparisons between Irish and UK populations indicated little genetic differentiation at microsatellite loci (Fst values 0-0.05), with gene flow (Nm) estimates of 12 migrants per generation. In contrast, genetic differentiation was higher for allozyme loci (Fst = 0.11; Nm = 2). Pairwise Fst values for microsatellite loci were positively correlated with geographic distance. This was not the case for the allozyme data. These results are discussed in the light of microsatellite data on populations from Holland, the Black Sea and the Great Lakes, North America.

9.15P

ESTIMATING POLLEN DISPERSAL CURVES IN TREE SPECIES WITH VARIOUS LIFE-HISTORY TRAITS

[1]Frederic Austerlitz, [2]Sylvie Oddou-Muratorio, [1]Etienne K. Klein,

[1]UPRESA CNRS 8079, Laboratoire Ecologie Systematique et Evolution, Bat 362, Universite Paris-Sud, 91405 Orsay cedex, France

[2]ONF Conservatoire Genetique des Arbres Forestiers, Campus INRA, 45160 Ardon, France

Gene flow through pollen is a major process that shapes genetic diversity in plants. The aim of this study was to estimate the mean distance of pollen dispersal and the dispersal curve for several tree species with contrasting life-history traits: social species or scattered species, insect or wind-pollinated, species from temperate and tropical forests. For this purpose, we performed for each species a paternity analysis on seeds sampled in a given population on several mother trees, using codominant molecular markers. In parallel we studied these species with the TwoGener method, which is based on the estimation of differentiation among the pollen pool fertilizing the sampled females. The advantage of this method is that it does not require the exhaustive sampling of the males of the population to estimate pollen flow. Both methods yield concordant results. (i) The estimated pollen dispersal curves are fat-tailed, yielding on one hand an excess of crossing between close individuals but on the other hand a non-negligible proportion of long-distance dispersal. (ii) Male reproductive success was highly variable among individuals, which lead to a lower effective density of reproducing males compared with the observed density. (iii) The dispersal curves obtained are consistent with the species' life-history traits.

9.16P

NUCLEOTIDE VARIATION AT THE FAH1 GENE OF *ARABIDOPSIS LYRATA*: COMPARISON BETWEEN *A. LYRATA* SSP. *PETRAEA* AND *A. LYRATA* SSP. *LYRATA*.

Daniel Balañá-Alcaide, Sebastian E. Ramos-Onsins, Monserrat Aguadé,

Universitat de Barcelona, Av. Diagonal 645, 08028 Barcelona, Spain

Arabidopsis lyrata, a close relative of the model species *A. thaliana,* is an outbreeding species present in both the Paleartic and Neartic regions. Since most population genetic models refer to outbreeding species, *A. lyrata* might be a more adequate plant model than *A. thaliana* to make inferences about evolutionary mechanisms and events from levels and patterns of nucleotide variation. The geographical split has fostered differentiation and resulted in two different subspecies: the European *A. lyrata* ssp. petraea and the North-American *A. lyrata* ssp. *lyrata.* A previous study of variation at the *Adh* region in this species revealed similar levels of variation in European and North-American samples. Another study based on one-individual samples from both continents revealed a reduction of variation in the North-American samples studied. The discrepancy between both studies might be due to the differing sampling strategies and/or to the low sample sizes. It could also reflect locus-specific patterns of variation. Here, we have studied nucleotide variation in an ~2.3-Kb fragment encompassing the *FAH1* gene, which encodes an enzyme of the phenylpropanoid pathway. Variation has been surveyed in two large random samples from Europe (Russia and Sweden) and another two from North America (Indiana and North Carolina). Our study reveals a significant genetic differentiation between populations from both the same and different continents. Estimated silent variation within North American populations is of the same order than within European populations, which would not be consistent with a strong effective population size reduction in North-America.

9.17P

CONTROL OF PLANT SPECIES DIVERSITY IN RIPARIAN CORRIDORS

[1]Åsa Bång, [2]Christer Nilsson, [1]Svante Holm,

[1]Dept of Natural and Environmental Sciences, Mid Sweden Univ., SE-851 70 Sundsvall, Sweden

[2]Landscape Ecology Group, Dept of Ecology and Environmental Science, Uminova Science Park, Umeå Univ., SE-901 87 Umeå, Sweden

The project aims at studying effects of river regulation on riparian plant populations. A previous study has shown that plant communities differ floristically between impoundments but remain similar within impoundments in a regulated river. The same pattern did not occur among plant species in a free-flowing river which instead showed a continuous change in species composition from the headwaters to the coast. This strongly suggests that the dispersal of plants is obstructed when dams are built on rivers. The present project will specifically study whether dams also affect the genetic diversity among and between populations of plant species. *Filipendula ulmaria* will be used as a first test species. A second question is whether tributaries have any impact on the distribution of genetic diversity of plant species within impoundments. A third question deals with the impact of seed and pollen dispersal on the genetic diversity among and between plant species populations. The project combines field sampling, field experiments and laboratory methods such as isoenzymes, microsatellites and other DNA-methods.

9.18P

CLIMATE CHANGE, BIODIVERSITY HOTSPOTS AND THE ENDANGERED TREE ALOE, *ALOE DICHOTOMA* (QUIVER TREE): THE GENETIC STATUS AND MANAGEMENT OF A FLAGSHIP SPECIES

[1,2]J M Bishop, [2]W Foden, [1]G Reeves, [2]G F Midgley

[1]*Leslie Hill Molecular Systematics Laboratory National Botanical Institute, Kirstenbosch Research Center, Private Bag X7, Claremont 7735, Cape Town, South Africa*

[2]*Climate Change and Biodiversity Research Group National Botanical Institute, Kirstenbosch Research Center, Private Bag X7, Claremont 7735, Cape Town, South Africa*

A complete understanding of the extent and distribution of genetic diversity within and among populations is essential for the development of effective conservation and management strategies with the aim of maintaining ecosystem biodiversity. Research by the Plant Biodiversity Section of the South African Country Study on climate change has shown that the Succulent Karoo Ecoregion of South Africa, the only arid biodiversity hotspot, could experience significant spatial shifts of areas of climatically suitable habitat by as early as 2050. Such changes are likely to cause significant biodiversity loss, unless new conservation strategies are developed to cope with this incipient threat. Range modelling and ecological assessment of the flagship Succulent Karoo species, *Aloe dichotoma*, has demonstrated the early warning signs of abiotically-induced stress in regions predicted to experience future anthropogenically mediated climate change. A complete understanding, therefore, of the extent and distribution of genetic diversity within and among extant populations of *A. dichotoma* is essential for the development of effective conservation and management strategies. On examining the effects of past and present climate change on the distribution and status of *A. dichotoma*, we report the utilisation of AFLP molecular markers for the quantification of current levels of genetic diversity, population structure and effective population size across the geographical range of this endangered species. Furthermore, because of the potential impact current and future patterns of climate change have been shown to have on the present-day distribution and demography of *A. dichotoma*, we identify areas of novel genetic variation. Together, these results are being used to assist the selection of areas where conservation activities are to be focused for the genetic management of the species. These results will act as a model for further genetic analysis of a number of important and threatened species in the light of the predicted effects of future climate change on the biodiversity of the Succulent Karoo ecosystem.

9.19P

GENETIC RELATEDNESS AND DIFFERENTIATION BETWEEN INDIVIDUALS IN POPULATIONS OF THE COMMON VOLE

Anetta Borkowska, Miroslaw Ratkiewicz

University of Bialystok, Swierkowa 20B, 15-950 Bialystok, Poland

Genetic structure, relatedness and differentiation between individuals were investigated in two populations of the common vole *Microtus arvalis* from NE Poland using 34 allozyme loci. Individual sampling sites for 33 voles in SG population and 14 voles in BR population were estimated using GPS. Relatedness between individuals (r) was assessed based on the genotype and allele frequencies at 11 polymorphic loci. Analysis revealed three family groups (female or male and its offspring) in SG and two family groups in BR population with $r>0.75$ between individuals in a group. Average relatedness values were very low in both populations ($r=-0.04$ and $r=-0.07$ in SG and BR, respectively). There were no correlation between pairwise relatedness and geographical distance between individuals in both populations ($r=0.05$; $P>0.05$ and $r=0.07$; $P>0.05$ in SG and BR, respectively).The effective population size estimated from genetic differentiation values between individuals was lower in the population with higher density (SG population: 4Dðó2=17.50) than in the BR population (4Dðó2= 43.26). Thus, 'neighbourhood size' (the product of density and the average squared axial parent-offspring distance) was 1.39 ind. in SG and 3.44 ind. in BR population.

9.20P

RESOURCES OF GENETIC VARIATION OF ISLAND ORCHID POPULATIONS FROM THE BIEBRZA NATIONAL PARK

Emilia Brzosko, Ada Wróblewska

University of Bialystok, Institute of Biology, Swierkowa 20B, 15-950 Bialystok, Poland

Populations of a few rare orchids species (*Cypripedium calceolus*, *Listera ovata*, *Cephalanthera rubra*, *Epipactis helleborine*) were genetically investigated in the Biebrza National Park (NE Poland). Orchids populations exist on the mineral islands among the widespread peat bogs and they are subjected to spatial environmental isolation. Levels of genetic variation differed among species, from the lowest in *Listera ovata* (P=9.4%, A=1.09) to the highest in *Cypripedium calceolus* (P=45.5%, A=1,73) or *Epipactis helleborine* (40.9%, A=2.80). The major factors shaping genetic diversity in orchids populations are biological characters of these species (the longevity of genets, breeding system, mode of reproduction) and history of mineral islands (they originated after the last glaciation). The importance above mentioned factors varied between species and populations. In all species studied the most of genetic variation existed within populations. The low Fst values with high gene flow may explain the maintenance of little genetic divergence among populations. Similarity of populations of a given species from the Biebrza region can also indicate their common origin.

9.21P

GENETIC STRUCTURE WITHIN IN A SPATIALLY SUBDIVIDED POPULATION OF ARABIDOPSIS LYRATA

Maria J. Clauss, Thomas Mitchell-Olds.

Department of Genetics and Evolution, Max Planck Institute of Chemical Ecology, Jena, Germany

Genetic variation was characterized in an undisturbed population of *Arabidopsis lyrata* subspp. *petraea*, a perennial herb closely related to *Arabidopsis thaliana*. In central Europe, *A. lyrata* is found in discrete populations edaphically restricted to soils derived from dolomitic rock. Within populations, individuals occur in dense patches on rocky outcrops. We collected a spatially explicit sample of 87 individuals and characterized these field collected individuals for microsatellite variability and nucleotide diversity at one functional locus (*Arabidopsis* trypsin inhibitor (ATTI). Microsatellite variation within this single population of *A. lyrata* was on the same order as a world-wide sample of *A. thaliana*. At the ATTI1 locus, the *A. lyrata* population had up to an order of magnitude more standing genetic variation than the species-wide sample of *A. thaliana*. However, there was little evidence to reject an equilibrium neutral model for either set of markers, and the spatial analysis detected little molecular population subdivision associated with ecological population structure. An analysis of quantitative genetic variation for herbivore defense and life history characters also showed little evidence of local differentiation within this genetically variable population.

9.22P

HUMAN IMPACT ON GENETIC DIVERSITY IN DOGWHELK POPULATIONS

Isabelle Colson, Roger N. Hughes

University of Wales Bangor, School of Biological Sciences, Deiniol Road, Bangor LL57 2UW, UK

Dogwhelks (*Nucella lapillus*) are intertidal marine snails particularly sensitive to tributyltin (TBT) pollution, which in extreme cases leads to female sterility. As a result, local extinctions have occurred in heavily polluted sites. After TBT was banned as an antifouling agent on small boats in 1987, populations across the UK have recovered and sites have been recolonised. Direct development and low rates of adult movement imply that dogwhelks should have a low dispersal ability. Despite this, population recovery has been relatively rapid. We aim to evaluate the effect of local extinctions/recolonisations on metapopulation genetics of *Nucella* across the United Kingdom, and address the question of the dynamics of recolonisation. Samples from recolonised sites and potential source populations were collected from three distinct geographical areas: SW England (Plymouth), SW Scotland (Isle of Cumbrae) and NE England (Tees estuary), and genotyped for 9 polymorphic microsatellite loci. Preliminary results on microsatellite genetic diversity and morphological variation in the Plymouth area seem to indicate that re-established populations do not show significant decrease in phenotypic or genetic variability. Evidence suggests that, at least in the Plymouth area, other factors contribute to the observed distribution of genetic diversity in dogwhelk populations. Patterns of recolonisation appear to follow a migrant-pool model, where colonising individuals originate from several distinct localities, suggesting that dogwhelks dispersal ability might be higher than what could be inferred from their life history.

9.23P

POPULATION DIFFERENCES IN GROWTH PATTERN, AND SHAPE AND STRENGTH OF ZEBRA MUSSEL SHELLS: RESPONSE TO PREDATOR PRESSURE?

M. Czarnoleski, P. Kubajak, T. Muller,

Jagiellonian University, Institute of Environmental Sciences, Gronostajowa 3, 30-387 Krakow, Poland

Organisms evolve different modes of antipredator defence to maximise lifetime fitness under the threat of predators. High mortality rate selects for earlier maturation at smaller body size and for the increase of resource allocation to reproduction at the expense of somatic growth later in life. Behavioural and morphological defence such as clumping, changes of body dimensions or strengthening of shells, adductors and byssi are known to be induced by predatorsin fish, crustaceans or molluscs. The antipredator strategies entail the costs limiting the simultaneous development of different defence modes and generate trade-offs between life histories. This work examines cross-population differences in growth pattern, and shell shape and strength in eight European populations of zebra mussels characterised by different rates of mortality. We test if these differences may be explained by defence reactions of *Dreissena polymorpha* to the varying across populations predator pressure. We show that the shell strength of mussels (measured by the force perforating a shell) was positively related to the observed mortality rate in population. Shell strength correlated positively with shell thickness. Mussels exposed to higher mortality rate tended to have less globous and more elongated shells. The shape of individual growth curves was changing with the population mortality rate; Bertalanffy's growth coefficient correlated positively and the asymptotic size negatively with a population mortality rate. The rates of growth and shell thickening were unrelated. The results indicate that zebra mussels may apply different antipredator strategies. They optimally adjust resource allocation between growth and reproduction, increasing the proportion of resources devoted to reproduction in more risky environment. They also strengthen shells and change shell dimensions, reducing the efficiency of feeding, capturing and handling of prey in crushing predators such as crayfish, fish or ducks.

9.24P

PHYLOGEOGRAPHY AND POPULATION GENETICS OF THE AFRICAN WILD SILK MOTH, *GONOMETA POSTICA*, AND IMPLICATIONS FOR HARVESTING IN SOUTHERN AFRICA

[1]Wayne Delport, [1]Paulette Bloomer, [2]J. Willem H. Ferguson,

[1]*Molecular Ecology and Evolution Program, Department of Genetics, University of Pretoria, Pretoria, 0002, South Africa*

[2]*Centre for Environmental Studies, Department of Zoology and Entomology, University of Pretoria, Pretoria, 0002, South Africa*

Several African moth species are economically exploitable but are only sporadically found in large numbers, both in time and in space. One of these is the African Wild Silk Moth, *Gonometa postica* whose silk is of exceptional quality. The moths show large inter-annual fluctuations in population size, which makes sustainable utilization difficult. Such fluctuations may be dependent on metapopulation processes and an understanding of the interaction between genetic and metapopulation-level factors affecting these moths would assist in understanding the survival of these species. We present the results from an annual survey of moths in southern Africa for 2002. In addition, we use samples collected during the survey to determine the distribution wide patterns of mtDNA genetic variation in the species. These data assist in determining the dispersal patterns of *Gonometa postica*, and provide an understanding of their broad scale population dynamics. In order to address local scale population dynamics we tested *Bombyx mori* microsatellites in *Gonometa postica.* We present the utility of *Bombyx mori* microsatellites in understanding the local movements of *Gonometa postica.* Finally, we consider the implications of our results in understanding the population dynamics of a species, and ultimately in providing guidelines for the harvesting of cocoons.

9.25P

MITOCHONDRIAL DNA VARIABILITY IN THE 'PAIRED' SPECIES OF LAMPREYS: *LAMPETRA FLUVIATILIS* (LINNAEUS, 1758) AND *LAMPETRA PLANERI* (BLOCK, 1784)

[1]R. Espanhol, [1]B. R. Quintella, [2]H. F. Gante, [3]M. C. Lucas, [4]P. R. Almeida, [4]M. J. Alves,

[1]*Instituto de Oceonagrafia, Faculdade de Ciências da Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal*

[2]*Centro de Biologia Ambiental, Museu Nacional de História Natural da Universidade de Lisboa, Rua da Escola Politécnica 58, 1269-102 Lisboa, Portugal*

[3]*University of Durham, School of Biological and Biomedical Sciences, South Road, Durham DH1 3LE, U. K.*

[4]*Universidade de Évora, Dep. Biologia, Lab. Biologia da Conservação, Apart. 94, 7002-554 Évora, Portugal*

Two species of *Lampetra* are recorded in Portugal, *L. fluviatilis* which is anadromous and parasitic when adult, and *L. planeri* which is non-migratory and non-parasitic and is thought to have evolved from the anadromous form. In the Red Book of Vertebrates of Portugal these two species are classified as rare, existing a considerable lack of knowledge about the distribution and bio-ecology. Field surveys using electrofishing have been carried out in northern and central rivers of Portugal to get information about the distribution and abundance of the two species. Electrofishing collected mainly ammocoetes, which are very difficult to discriminate morphologically. Therefore, a study was initiated to provide genetic markers for taxon diagnosis. A total of 2020 bp of the mytochondrial genome were sequenced from the cytochrome *b* gene, and ATPase subunits 6 and 8 for 43 lampreys (40 ammocoetes, 2 transforming specimens and 1 adult of *L. planeri*) collected in 13 localities. Besides the Portuguese specimens, sequences from three adults of *L. fluviatilis* and one of *L. planeri* collected in the Ure River (Ouse River basin, North England) and the sequence of one adult of *L. fluviatilis* collected in the Garone estuary (France) available in the EMBL database were included in the analysis. Neighbour-joining and maximum parsimony analyses revealed geographic structuring of the Portuguese samples. Adults of lampreys collected in France and North England were placed in the same clade, independently of their specific status. Despite the low number of adults analysed, these results raise the hypotheses that hybridization may occur between the two species or that these two forms may be ecological modifications of one and the same gene pool, questioning the traditional view that these two forms are taxonomically distinct. ATPase was sequenced for seven additional specimens from each site, and mtDNA variation was further characterized through a hierearchical analysis of molecular variance (AMOVA) and the construction of a minimum spanning network.

9.26P

GENETIC STRUCTURE OF TWO GASTROPOD SPECIES IN AN ALLUVIAL HABITAT

[1]G. Evanno, [1]J. Goudet, [2]E. Castella,

[1]*University of Lausanne, Biology bulding, IE-bsg, 1015 Lausanne, Switzerland*

[2]*Université de Genève, LEBA, 18 chemin des Clochettes, 1206 Genève, Switzerland*

Alluvial ecosystems exhibit a mosaic of habitats whose biodiversity is mainly driven by the frequency and intensity of floods. At the genetic level, populations that occur in frequently flooded areas are supposed to bear more gene flow than those occurring in similar but not flooded habitats. To investigate this issue we have studied populations of the gastropods *Radix balthica* and *Planorbis carinatus* living in old meanders disconnected from the river Ain (France). Each old meander is similar to a set of independent ponds. Snails were sampled in 3 ponds close to the river and regularly flooded as well as in 3 sites located upstream within the meanders and not recently flooded. Individuals were genotyped using AFLP markers (Amplified Fragment Length Polymorphism). Results allowed us to infer the patterns of gene flow in a naturally disturbed habitat.

9.27P

MAINTENANCE OF ALLELIC DIVERSITY IN SMALL POPULATIONS

[1]J. Fernández, [2]M. A Toro, [3]A. Caballero

[1]*Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Madrid, Spain*

[2] *Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Madrid, Spain*

[3]*Universidad de Vigo. Facultad de Ciencias, 36200 Vigo, Spain*

To assure the evolvability, i.e. the ability for adapting to new environmental conditions, as well as to guarantee the reintroduction into the wild of captive populations, high levels of genetic diversity should be maintained. As the usual genetic richness measure is the expected heterozygosity of the population, or gene diversity (GD), most studies, especially in the conservation field, have been devoted to find optimal strategies to maximise this parameter. However, little attention has been paid to the evolutionary consequences of allelic diversity (AD), i.e. the number of alleles kept by the population, or to the development of strategies to manage it. We describe some methods to account for the allelic diversity in a population kept in captivity, using information from neutral molecular markers. Using computer simulations we show that the optimal strategies directed to the maximisation of GD keep levels of AD as high as strategies based on AD itself. Because the maximisation of GD also minimises the levels of inbreeding, this should be the strategy of choice in any population management programme.

9.28P

LOCAL GENETIC POPULATION STRUCTURE FACILITATES CHOICE FOR DISSIMILAR EXTRA-PAIR MATING PARTNERS IN BLUE TITS (*PARUS CAERULAEUS*)

Katharina Foerster, Bart Kempenaers

Max Planck Research Centre for Ornithology, P.O. Box 1564, D-82305 Starnberg (Seewiesen), Germany

Individual genetic diversity (measured as average heterozygosity) is a strong fitness predictor, also within outbred populations. Mating with individuals carrying similar alleles can be disadvantageous, as offspring with lower heterozygosity are of lower reproductive value. If individuals can increase the reproductive value of their offspring by producing more heterozygous young, we expect that this will drive mate choice for genetically dissimilar mates. In species where social mate choice is restricted, extra-pair copulations provide a potential mechanism to increase the genetic diversity, and hence fitness, of the offspring. This would be in accordance with the idea, that males and females engage in extra-pair copulations to increase the genetic quality of their progeny. Here, we show that the local genetic structure of a generally outbred blue tit population enables individuals to distinguish between more and less genetically similar potential copulation partners: genetic similarity between breeding males and females decreased with breeding distance. This structure facilitates active choice for a genetically less similar partner (by choosing individuals that breed further away), without a mechanism of self reference. We further show that female blue tits increase the heterozygosity of their progeny through extra-pair matings with non-neighbouring males. Females thereby produce offspring of higher reproductive value, because less inbred blue tits have increased survival chances and higher reproductive success. Our data support the idea that females mate multiply to obtain compatible genes for their offspring, thereby avoiding the negative effects of inbreeding.

9.29P

MICROGEOGRAPHIC HETEROGENEITY IN SPATIAL DISTRIBUTION AND GENETIC STRUCTURE OF GREY MOUSE LEMURS (*MICROCEBUS MURINUS*)

[1]Tina Fredsted, [2]Cino Pertoldi, [1]Jens Mogens Olesen, [3]Manfred Eberle,
[3]Peter M. Kappeler

[1]University of Aarhus, Ny Munkegade Building 540, 8000 Aarhus, Denmark

[2]National Environmental Research Institute, Grenåvej 12, 8410 Rønde, Denmark

[3]German Primate Center, Department of Behavior & Ecology, Kellnerweg 4, D-37077 Göttingen, Germany

The objectives of our study were to elucidate the spatial distribution, genetic structure and dispersal patterns at a microgeographical scale in a small nocturnal primate, the solitary grey mouse lemur (*Microcebus murinus*) to contribute comparative information for the interpretation of social behavior and evolutionary reconstructions of primate social systems. Tissue samples from 205 grey mouse lemurs were obtained along transects and in three grid systems covering more than 12 km2 in Kirindy Forest in western Madagascar. The frequency distribution of 22 mtDNA D-loop haplotypes was highly skewed. Nine haplotypes were unique to males, indicating male-mediated gene flow from surrounding areas. Mouse lemurs were not evenly distributed in the continuous forest. The geographic distribution of haplotypes revealed that males were consistently dispersed as well as a tendency towards spatial aggregation of females with a particular haplotype, indicating female philopatry. Females moved around less and spatial autocorrelation between genetic and geographic distances was higher in females. However, some females behaved differently; similar-typed females were widely dispersed in smaller clusters, indicating female mobility and occasional active long-term dispersal. The lack of concordance between mtDNA haplotype phylogeny and the geographical distribution of haplotypes supported this interpretation. We found a more complex dispersal pattern in both sexes than previously recognized on smaller spatial scales with important consequences for interpreting population structure and conservation planning.

9.30P

EFFECT OF FERTILITY INHERITANCE ON N_E AND COALESCENT TREES

[1]E. Heyer, [2]A. Austerlitz, [1]A. Sibert

[1]Eco-Anthropologie, Musée de l'Homme, 17 pl du Trocadéro, 75116 Paris, France

[2]Laboratoire Ecologie Systematique et Evolution, Universite Paris-Sud, 91405 Orsay, France

In recent studies, we have shown that the transmission of reproductive success from parent to offspring causes a 10- to 20-fold reduction of effective population size (Ne) in a human population. By transmission of reproductive success or fertility inheritance, we mean that members of families with a large number of effective children (children that have a genetic contribution to the population), tend themselves to have a large number of effective children. This social factor was measured in a population of Quebec and explains the high frequency of some inherited disorders in this population This population (current census size N=300000) was founded 12 generations ago by a limited number of immigrants. We showed by simulation that Ne is divided by one order of magnitude by this transmission of reproductive success: from 17,000 to 900. In parallel, we have recently developed a theoretical framework for this phenomenon in a constant size population (Sibert et al, 2002) when levels of transmission are equal to those measured in the Quebec population. This formalization enables us to describe the impact of this fertility transmission on gene genealogies: (i)it reduces the total size of the Tree and the Tmrca (ii) it changes the shape of the tree that looks stare-like even in a stationary population (iii) it induces imbalance in the coalescent tree. In conclusion this 'vertical transmission' of fertility has a strong impact on genetic diversity and could thus be detected in natural populations.

9.31P

HETEROZYGOTE DEFICIENCY IN JUVENILE PLAICE (*PLEURONECTES PLATESSA*) : EVIDENCE FOR INBREEDING

[1]G. Hoarau, [2]H.W. Van der Veer, [3]A.D. Rijnsdorp, [4]W.T. Stam, [5]J.L. Olsen

[1]Department of Marine Biology, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands

[2]Netherlands Institute for Sea Research, PO Box 59, 1790 AB Den Burg Texel, The Netherlands

[3]Netherlands Institute for Fisheries Research, PO Box 68, 1970 AB IJmuiden, The Netherlands

[4]Department of Marine Biology, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands

[5]Department of Marine Biology, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands

Heterozygote deficiency is relatively common in marine organism such as bivalves and fish. For most studies, the cause for the departure from Hardy-Weinberg equilibrium (HWE) remains unclear. Potential causes include sampling artefacts (Wahlund effect or relatedness), genotyping errors (null alleles), and biological processes (selection or inbreeding). Relatively high Fis values were observed in a microsatellite based study of plaice, a flatfish which forms an important component of North Sea fisheries. To understand the causes of departure from HWE in plaice, we examined biweekly cohorts of juveniles collected from two nursery grounds (Dutch Wadden Sea and Iceland) to determine the relationship of Fis and age of cohort. Related individuals were present in at least two cohorts and evidence for inbreeding was found for almost all samples. The results indicate that inbreeding (mating between genetically related individuals) is the primary cause of high observe Fis values. This finding was unexpected and indicate that our perceptions of mating behaviour in plaice are suspect. Inbreeding in plaice could be related to fisheries pressure and our results suggest that plaice population might be suffering from inbreeding depression.

9.32P

POPULATION GENETIC STRUCTURE OF THE CAPERCAILLIE (*TETRAO UROGALLUS*) IN THE SWISS ALPS

[1]G. Jacob, [1]F. Gugerli, [1]W. Suter, [2]B. Schmid,

[1]Swiss Federal Research Institute WSL, Zuercherstrasse 111, 8903 Birmensdorf, Switzerland

[2]Institute of Environmental Sciences, University of Zurich, Winterthurstrasse 190, 8057 Zurich, Switzerland

The capercaillie (*Tetrao urogallus*) is a grouse species distributed continuously along the taiga forest, from Sweden to China, and in isolated units in Central and Southern Europe, where the species experiences a severe decline since the 20th century. Studying the dynamic of the capercaillie in a human altered landscape will help to determine the effects of habitat fragmentation on the dynamic of the species. A research project at the Swiss Federal Research Institute (WSL) aims at developing a spatially explicit population model for the capercaillie in the Swiss Alps based on demographic, geographic and genetic data. I investigate the structure of the population and the levels of gene flow among sub-populations by genotyping 600 individuals from the extant species distribution in the Swiss Alps. Combining genetic, demographic and geographic data will allow to study the factors affecting the distribution and the sustainability of the species in a fragmented landscape. The resulting model will be validated using a past genetic reference inferred from museum specimens and aerial photographs from the beginning of the century.

9.33P

GENETIC CONSEQUENCES OF HABITAT FRAGMENTATION IN SWEDISH POPULATIONS

[1]Markus Johansson, [2]Craig Primmer, [3]Juha Merilä

[1]*Dep. of Population Biology, EBC, Uppsala University, Norbyvägen 18 d, 75426 Uppsala, Sweden*

[2]*Department of Ecology and Systematics, PO Box 65 (Biocenter 3, Viikinkaari 1), FIN-00014 University of Helsinki, Finland*

[3]*Ecological Genetics Research Unit, Department of Ecology and Systematics, PO Box 65 (Biocenter 3, Viikinkaari 1), FIN-00014 University of Helsinki, Finland*

One of the most acknowledged causes of declines in size and number of natural populations is human induced habitat fragmentation. Habitat fragmentation leads to an immediate reduction in population size due to the destruction of the original habitat. However, the long-term population viability might also be jeopardized as a consequence of loss of rare alleles both instantaneously and continuously through increased influence of genetic drift and reduced gene flow. We have studied the genetic status in populations over a wide range of Scandinavian habitat types in three different regions (over 100 populations) of spatially and chronologically dissimilar history of habitat fragmentation using microsatellite markers. We found a significant difference between fragmented and control populations in the region with the most extensive and oldest history of land cultivation. However in regions with less intense and shorter agricultural history, we did not find any differences between fragmented and control populations. These results suggest that genetic consequences of fragmented populations are time and intensity dependent.

9.34P

CAN FLUCTUATING ASYMMETRY BE USED AS A RELIABLE TOOL IN CONSERVATION BIOLOGY?

D. Joubert, R. Bijlsma

Evolutionary Genetics Group, University of Groningen, P.O. Box 14, 9750 AA Haren, Netherlands

Increase in fluctuating asymmetry (FA) is thought to reveal the presence of both genetic and environmental stress during development. It is also thought to be an indirect measure of fitness of individuals or populations. Therefore, FA has been advocated as a reliable and sensitive monitor for the well-being of populations under stress and as such could serve as a decisive tool in conservation biology. Several studies have shown a positive relation between FA and stress. However this positive relation does not seem unequivocal. Using *Drosophila* as a model organism my study has focused on the relation between inbreeding and FA, both without and in combination with environmental stress. I will present the results of several experiments that show very mixed results: an increase in FA is observed in some experiments and non in others, some traits but not necessarily the same are affected but others not. Environmental stress can complicate the situation even more. Overall my results suggest that increase in FA may indicate the presence of problems but it is surely not a reliable tool.

9.35P

ADAPTATIONS TO LABORATORY CONDITIONS OF THE TROPICAL BUTTERFLY *BICYCLUS ANYNANA*

Rinny E. Kooi, Paul M. Brakefield

Evolutionary Biology, University of Leiden, P.O. Box 9516, 2300 RA Leiden, The Netherlands

The adaptation to laboratory (food plant) conditions of the polyphenic tropical butterfly *Bicyclus anynana* from Malawi was examined as indications for such adaptation were found in a stock which was kept in the laboratory since 1988. This stock and a new one obtained in 1999 from the same field locality were compared in oviposition and larval performance experiments. Significant differences were obtained in the acceptability and suitability of four food plants species, as well as in the environmental effects in the wing pattern induction. This suggests that changes in life history traits have evolved in the laboratory stock since 1988. This information and the results of similar experiments might be valuable for the re-establisment of animals in the wild from captive stocks.

9.36P

HETEROZYGOSITY AND FITNESS IN *ECHIUM VULGARE* (BORAGINACEAE)

[1]G. Korbecka, [2]P.G.L. Klinkhamer, [2]K. Vrieling

[1]*University of Newcastle, School of Biology, Ridley Building, Newcastle upon Tyne, NE1 7RU, UK*

[2]*Leiden University, Institute of Biology Leiden, P.O. Box 9516, 2300 RA Leiden, The Netherlands*

Echium vulgare is a tetraploid plant. Previous experiments have shown no effects of inbreeding depression on seed set. Averaged over 10 genotypes, selfing resulted in as many seeds as outcrossing. However, selfed offspring performed worse during reproduction. They had lower seed set and sired fewer seeds on other plants. Such late acting inbreeding depression may be important in the field because of limited seed dispersal of *E. vulgare*. Seeds fall next to the mother plant and therefore half sibs are likely to grow next to each other and mate with each other. Firstly, I will test the hypothesis that plants growing within the groups in the field are genetically more similar to each other than to plants growing in a distance in order to support my prediction about consequences of limited seed dispersal. Secondly, I will present data on the heterozygosity-fitness correlation to verify whether inbreeding depression plays a role in *E. vulgare* in the field.

9.37P

GENETIC VARIATION AND ADAPTIVE ABILITIES OF NATURAL AND CAPTIVE MALLORCAN MIDWIFE TOAD STOCKS

[1]Femmie J.L. Kraaijeveld-Smit, [1]Robin D. Moore, [1]Richard A. Griffiths,
[2]Trevor J.C. Beebee

[1]*DICE, University of Kent at Canterbury, Canterbury, CT2 7NS, UK*

[2]*School of Biological Sciences, University of Sussex, Falmer, BN1 9QG, UK*

The Mallorcan midwife toad *Alytes muletensis* is endemic to the Mediterranean island of Mallorca, where it occurs in about 19 isolated populations. Six of these populations stem from successful reintroductions following a captive breeding programme initiated in the 1980s. >From a conservation perspective, it is important to test whether such reintroduced populations have suffered any genetic bottlenecking as a result of the small number of founders used to start the captive colonies. We compared the predator responses of naive tadpoles from a reintroduced (i.e. potentially bottlenecked) population to a natural population. The bottlenecked population showed no reduction in antipredator responses to the snake *Natrix maura*, the principle predator of the toad. Tadpoles from both populations reduced activity and had deeper tail-muscles when exposed to predator-conditioned water compared to tadpoles in control water. Heterozygosity levels at 10 microsatellite loci were positively correlated to tail muscle depth. We also investigated genetic diversity in five natural populations and one reintroduced population. Populations were genetically highly differentiated but varied in their genetic variability. It is reassuring that reintroduced *A. muletensis* appear to have retained antipredator responses and a relatively high degree of genetic variability despite multiple generations of captive breeding.

9.38P

CHARACTERISING A MARINE INVASION: GENETIC DIVERSITY OF INDIGENOUS AND INTRODUCED POPULATIONS OF THE MOLLUSC *CREPIDULA FORNICATA*

Inken Kruse, Lise Dupont, Dugald McGlashan, Frédérique Viard

Evolution et Génétique des Populations Marines, Station Biologique de Roscoff, UMR-CNRS 7127, Place Georges Teissier, BP 74, 29682 Roscoff cedex, France

The hermaphroditic gastropod *Crepidula fornicata* has been introduced from the American Atlantic coast to Europe in the late 19th century. Since the spread of *C. fornicata* along European coastlines has been well recorded, genetic study of this species offers the opportunity to trace historical processes of a marine invasion and subsequent dispersal. We analysed mtDNA and microsatellite polymorphisms of *C. fornicata* populations along the species' distributional range in North America and Europe. The aims of this study were to compare haplotypes between the continents and to reveal (i) the relative levels of genetic diversity of introduced and native populations, (ii) the differentiation among European and among American populations and (iii) the likelihood or contribution of repeated introductions. Interestingly, our first results reflect no founder effect for European populations. Both introduced and native populations exhibited high genetic diversity and low differentiation. This may be explained by the occurrence of multiple introductions, the species' high dispersal potential by broadcasting pelagic larvae and a huge number of founding individuals. Since *C. fornicata* is both a very successful marine invader and a competitor of economically important species, estimates for its evolutionary potential are strongly needed to develop recommendations for its management.

9.39P

SIBLING SPECIES IN THE COSMOPOLITAN MARINE POLYCHAETE *SCOLOPLOS ARMIGER*: MAY DIVERGENCE IN DEVELOPMENTAL MODE CAUSE SYMPATRIC SPECIATION?

[1]Inken Kruse, [2]Thorsten B. H. Reusch, [3]Vicky Schneider, [4]Frank Thiermann, [5]Karsten Reise

[1]Evolution et Génétique des Populations Marines, Station Biologique de Roscoff, UMR-CNRS 7127, Place Georges Teissier, BP 74, 29682 Roscoff cedex, France

[2]Max Planck Institute for Limnology, Department of Evolutionary Ecology, Postfach 165, 24306 Plön, Germany

[3]Section Animal Ecology, Institute of Evolutionary and Ecological Sciences, University of Leiden, P.O. Box 9516, NL-2300 RA Leiden, The Netherlands

[4]Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Martin-Luther-King-Platz 3, 10146 Hamburg, Germany

[5]1Alfred-Wegener-Insitut für Polar- und Meeresforschung, Wattenmeerstation Sylt, 25992 List, Germany

For the common, cosmopolitan polychaete *Scoloplos armiger* (O. F. Müller, 1776) two developmental modes exist in the North Sea region. In addition to direct, holobenthic development out of egg cocoons, well-known to occur on intertidal flats, pelagic larvae emerge from subtidal specimens. Different approaches and methods were used to assess the taxonomic status of intertidal and subtidal *S. armiger*: morphological comparison, application of genetic markers, cross breeding experiments and experiments on physiological performance. All results indicate that there are two sympatric sibling species in S. armiger, *Type I* living in the intertidal zone and *Type S* living subtidally. Spermatozoa of intertidal males are significantly different to those from subtidal males. It is suggested that deviating sperm morphology may cause the reproductive down at the fertilization stage. Physiological comparison of intertidal and subtidal *S. armiger* may indicate ecological speciation. Tolerance against sulphide and hypoxia were both lower in subtidal than in intertidal specimens. This correlates with a 5 to 10-fold lower sulphide concentration at subtidal compared to intertidal sites. It is discussed how the present-day situation with distinct, sympatric species occurring in geographic overlap while exhibiting segregation by habitat may have evolved, resulting in different speciation scenarios for *S. armiger*.

9.40P

EVOLUTION OF GENETIC DIVERSITY DURING THE INVASION PROCESS OF THE EUROPEAN WEED *SENECIO INAEQUIDENS* (ASTERACEAE): GENETIC MARKERS VERSUS QUANTITATIVE GENETIC VARIATION

L. Lafuma

University of Montpellier, Place Eugène bataillon, cc065, ISEM, 34 095 Montpellier

One important component that may influence the success of a species as an invader is its genetic composition. The amount and distribution of genetic diversity can have profound effects on whether an invasive species will continue to spread. For instance, reduced genetic diversity may limit the ability of the population to evolve. Theory predicts that colonization of new areas will be associated with population bottlenecks that reduce within-population genetic diversity and increase genetic differentiation among population. This is particularly the case for weedy species introduced to new areas: introduced populations often descend from a few founders and are completely isolated from source populations. However less reduction in genetic variation may occur if either recent populations are linked to source populations or large population sizes are maintained following introduction in outbreeding species. The plant *Senecio inaequidens* DC (Asteraceae) is a good model for studying the effects on genetic variation during the invasion process. This weed, native of South-Africa, has been introduced in Europe in the beginning of the twentieth century. Besides, historical data of the invasion process are available in Europe for two transects of colonization. Six populations of the self-incompatible invasive species *S. inaequidens* were studied to compare evolution of genetic diversity at two scales: (1) between native and introduced populations (not linked), (2) between recent and old populations (linked) of two transect of colonization in Europe. Comparisons of both neutral and quantitative characters are used to determine the relative importance of natural selection and migration in the process of differentiation. We have examined the amount and distribution of molecular genetic diversity that exists with isozymes and chloroplastic DNA microsatellites. Next, using a common garden experiment we have determined the amount and distribution of quantitative variation in two environments for several characters (growth-, phenology-, fitness- related traits).

9.41P

IS THERE CASTE-SPECIFIC INBREEDING DEPRESSION IN THE ANT *FORMICA EXSECTA*?

Cathy Liautard, Emma Vitikainen, Liselotte Sundström

University of Helsinki, Institute of Ecology and Systematics, PO Box 65, 00014 Helsinki, Finland

The rate of habitat fragmentation caused by human activities is accelerating with severe consequences for animal life history traits such as dispersal and breeding patterns. It will increase the risk of inbreeding, and potentially the rate of inbreeding depression. In social insects inbreeding depression has been hypothesized to have a stronger effect than in other animals. Owing to their social mode of life, selection may act against inbreeding at the individual as well as at the colony level. Previous data have shown that in single-queen colonies of *Formica exsecta*, workers are inbred to the extent that approximately 40% of them are the offspring of brother-sister matings, whereas no significant inbreeding was found in resident queens. As workers and queens are issued from the same batch of diploid eggs, this suggests selection against inbred queens. This difference in inbreeding between the two castes of diploids could arise in two ways. First, colony can specialise for sex allocation according to the relatedness between the queen and her mate. Second, inbred gynes (young unmated queens) have lower fitness and may therefore be less successful during colony foundation. To test the latter hypothesis we compared inbreeding level of young queens before they start a new colony with that of queens in established mature colony. Additionally, as we know the age of our colonies, we analysed the correlation between colony age and queen heterozygosity. Finally, inbreeding depression may be expressed at the colony level such that more inbred workers may decrease colony performance. We therefore compared colonies with different levels of inbreeding with respect to their productivity.

9.42P

GENETIC VARIATION AND PHENOTYPIC PLASTICITY IN *LEPTINOTARSA DECEMLINEATA* UNDER DIFFERENT SELECTION PRESSURES

Leena Lindström, Sanna Ahoniemi, Alessandro Grapputo, Anne Lyytinen,
Johanna Mappes

University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FIN-40014 University of Jyväskylä, Finland

Invasive pest species provide us an opportunity to study genetic variation linked to selection pressures in the natural populations. First as they are invading to new areas they have to adjust to new temperature regimes. Secondly, they have to adjust to human induced selection by pesticides. And thirdly, invasive herbivores might have to adjust also to a new variety of cultured host plant species as they invade new countries. All these selection pressures create different forms of selection, which are expected to shape the individuals. We used Colorado potato beetle *Leptinotarsa decemlineata* as a study organism. First we compared the pesticide resistance of Polish, Estonian, Russian and Finnish (recent invasion) populations which have different historical record of the beetle. We used bi-PASA PCR to detect the mutations conferring resistance to two pesticides: permethrins and aziphos-methyls. The frequency of alleles conferring resistance to permethrin was highest in Polish, and declined for Estonian and Russian populations, which suggests that the Polish population has experienced highest selection. However, resistance to aziphos-methyls was in overall high and similar in all populations. In laboratory the resistance to permethrins declined suggesting a cost of carrying the resistance. Furthermore, beetles collected from the field, which were homozygotes for the resistance to permethrins, were smaller in size. Additionally we reared beetles from Russian population in two different temperatures on three different potato varieties. This experiment suggests that there was enough genetic variability (measured as full-sib analysis) in development times in cold temperatures implying that there is potential for the beetle to adapt further to cooler climates. Host plant variety affected size at emergence but not the development times.

9.43P

QST >> FST IN A MARINE BIVALVE; IMPLICATIONS FOR MARINE NATURE CONSERVATION

P.C. Luttikhuizen

University of Amsterdam, Kruislaan 318, 1098 SM, Amsterdam, The Netherlands

Nature conservation of marine biodiversity is increasingly moving towards the protection of refuge areas, called 'Marine Protected Areas' or 'No-Take Zones'. The exploited areas are to be recolonized from these MPA's, that thus function both as recruitment source and biodiversity reserve. This strategy implicitly assumes that, first, effective dispersal rates will be high and second, that intraspecific genetic differentiation for ecologically important characters is limited at the spatial scale of MPA's and their exploited matrix. The life cycle of many marine taxa involves one or several free-swimming life stages and predicts that these two assumptions may be valid. Empirical data refuting the first assumption (large effective dispersal) in such taxa have accumulated over the last decade. The second assumption was tested in the marine bivalve *Macoma balthica*, which has a free-swimming larval phase of 2-5 weeks. The approach we used was to contrast quantitative with neutral molecular genetic variation within and between the western Dutch Wadden Sea and adjacent North Sea sites by rearing the bivalves in the laboratory and studying allozyme and mitochondrial DNA sequence variation. The spatial structuring of genetic variation between seas was much larger for the quantitative genetic trait (shell shape; Qst = 0.416) than for the molecular markers (Fst = 0.000 to 0.022). Two selection factors possibly involved in maintaining the spatial differentiation in shell globosity are predation by shorebirds and burying capacity in different sediment structures, as shown by field observations and laboratory experiments. Ecologically relevant genetic variation can thus be strongly differentiated over relatively small spatial scales, even in high-dispersal marine taxa. These findings are important for the MPA debate, as harvesting from particular habitats may decrease intraspecific biodiversity.

9.44P

GENETIC STRUCTURE ESTIMATION OF ATLANTIC *THUNNUS OBESUS* BY MTDNA ANALYSIS: A CONSIDERATION FOR MANAGEMENT

P. Martinez, R. Zardoya,

Museo Nacional Ciencias Naturales (CSIC). José Gutiérrez Abascal,2 28006 Madrid, Spain

The bigeye tuna *T. obesus* Lowe 1839 is a panoceanic migrating species inhabiting tropical and subtropical waters. Identification of its biological units or stocks intraoceanically is fundamental for management. However, intraspecific genetic diversity and population substructure have been poorly studied within the Atlantic. Hereby, approximately 250 individuals were obtained from the BETYP 2001 *T. obesus* program and from commercial Albacora 2002 operations. mtDNA analysis from partial (D-loop) control region sequences (409bp) were used for genetic population simulations; outgroups from Pacific *T. obesus*, other tuna and related counterparts within the family were considered. At least three main phylogenetic clades I-III resulted where no correspondence with geography was observed. Some significance may be present between the FST values of the most geographically expanded samples. The effect of a bottleneck on pairwise genetic distances for this highly migrating species was evaluated together with further population estimations.

9.45P

GENETIC VARIABILITY AND STRUCTURE IN THE ENDANGERED SPANISH IMPERIAL EAGLE (*AQUILA ADALBERTI*)

B. Martinez-Cruz, J.J. Negro, J.A. Godoy,

Estacion Biologica de Doñana (CSIC), Avda. Maria Luisa s/n, 41013 Sevilla, Spain

The endangered Spanish imperial eagle, *Aquila adalberti*, is an example of a small population that has suffered from both fragmentation and size reduction mainly due to human pressure. Here we describe the current genetic status of the population in 79 individuals from all the distribution range, adscribed a priori to five breeding nuclei. First, we describe the levels of genetic variability in the Spanish imperial eagle population using the hypervariable domain of the mitochondrial control region and 18 microsatellite markers. Levels of genetic variability in the Eastern imperial eagle, Aquila heliaca, the nearest extant relative, have also been estimated. Neither allelic richness nor levels of heterozygosity differed among the breeding nuclei of the Spanish imperial eagle (Kruskal-Wallis test, $P>0.05$). Haplotype diversity was lower in the Spanish than in the Eastern imperial eagle (Welch test, $P<0.05$). No signal of a recent genetic bottleneck was detected in the current Spanish imperial eagle population ($P=0.15190$, Wilcoxon rank test). In addition, microsatellites were used to investigate the genetic structure of the Spanish imperial eagle using both distance-based and model-based approaches. Low although significant Fst values ($P<0.05$) were obtained that were congruent with a model of isolation by distance. Fst and exact tests of population differentiation showed differentiation among PND and all the remnant breeding nuclei. In the other hand, a bayesian approach clearly structures the Spanish imperial eagle into two subpopulations: Parque Nacional de Doñana (PND) and the remaining breeding nuclei (RBN). Individuals were assigned with a high probability to one of the subpopulations. We detected two migrants and two admixed individuals. We discuss how management strategies should imply the maintenance of current genetic variability and the connection of the smallest nucleus of PND to RBN to prevent its genetic depauperation.

9.46P

CHLOROPLAST MICROSATELLITE EVOLUTION IN CONIFERS: MEASURES OF GENETIC DIVERSITY AND THE EFFECT OF HOMOPLASY

Miguel de Navascués, Brent C. Emerson

School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK

Chloroplast microsatellites (cpSSR) have been widely used in population studies of pines in the last years. However, the haplotype configurations found suggest that could have high levels of homoplasy thus limiting the power of this molecular marker. A coalescent-based computer simulation was used to explore the influence of homoplasy in measures of genetic diversity based on cpSSR. The conditions of the simulation were determined to fit isolated populations originating from the colonisation of one single haplotype into an area left available after the glacial retreat. Simulated data were compared with empirical data available in the literature for *Pinus* species which have expanded north after the last glacial maxima. Mutation rates appear to be greater than previous estimates. In the evaluation of genetic diversity, homoplasy was found to have little influence in Nei's unbiased haplotype diversity while Goldstein's average distance among individuals highly underestimated diversity. Appropriate sample sizes for evaluation of genetic diversity are also discussed.

9.47P

SALINITY TOLERANCE OF *D. MAGNA* POPULATIONS IN THE RECENT HISTORY OF GROSSER BINNENSEE INFERRED FROM THE EGG BANK.

Raquel Ortells, Thorsten Reusch, Winfried Lampert

Max Plank Institute for Limnology, August Thienenmann Strasse, 2. 24306 Ploen, Germany

Resting eggs from aquatic zooplankton accumulate in the sediment of lakes and can remain viable for years, representing the genetic pool of species and genotypes which were present in the lake along time. As they are formed at different times and under different conditions, they provide the population with a 'memory from the past' and the possibility to maintain particular environmental responses in fluctuating habitats. Grosser Binnensee is a coastal shallow lake that drains into the Baltic Sea. It has suffered drastic salinity fluctuations in the last decade. Before 1991, the lake was slightly brackish. The dominant population of daphnids at that moment was *D. magna*, which disappeared from the lake after the inclusion of big amounts of seawater. The connection to the Baltic Sea was closed afterwards and the lake then became fresh. *D. magna* was still found after this change, but now, their populations are only present in the lake during several weeks in spring, and then, they are eventually replaced by smaller daphniids. By hatching *D. magna* resting eggs (ephippia) from vertical sediment cores it is possible to recover populations produced in the lake along time. We will test the variability of responses to salinity in the water column and in the resting egg bank populations by measuring hatching success and fitness at different salinity conditions. In addition, with the use of microsatellite markers, we will measure the levels of genetic diversity in both the resting egg bank and the water-column population. The objective is to determine the role of the resting egg bank in providing the genetic diversity needed for the variability of responses in an unpredictable environment. By achieving this, we will be opening new questions on the community structure dynamics of the Grosser Binnensee.

9.48P

ASSESSING THE GENETIC STRUCTURE OF THE EGYPTIAN MONGOOSE IN PORTUGAL

[1]Iris Pereira, [2]Catarina Ginja, [3]Michael W. Bruford, [4]Margarida Santos-Reis,

[1]*Centro de Biologia Ambiental, Faculdade de Ciências da Universidade de Lisboa, Edifício C2 - 3°Piso, Departamento de Biologia Animal, Campo Grande, 1749-016 Lisboa*

[2]*Centro de Biologia Ambiental, Faculdade de Ciências da Universidade de Lisboa, Edifício C2 - 3°Piso, Departamento de Biologia Animal, Campo Grande, 1749-016 Lisboa*

[3]*Cardiff School of Biosciences, Cardiff University, Main Building, Park Place, PO Box 9155, Cardiff CF 10 3TL Wales, UK*

[4]*Centro de Biologia Ambiental, Faculdade de Ciências da Universidade de Lisboa, Edifício C2 - 3°Piso, Departamento de Biologia Animal, Campo Grande, 1749-016 Lisboa*

The Egyptian mongoose (*Herpestes ichneumon* L., 1758) is a small-sized carnivore of African origin with an European range largely restricted to the SW Iberian Peninsula. In Portugal its present range has well extended towards north but the current limit is still unknown. Few studies concerning the species have been carried out in the Iberian Peninsula; hence a number of aspects about the mongoose ecology, genetics, population status and range are still poorly understood. In 2002 a project started in order to study the genetic structure, the geographical and dispersal patterns and the phylogeny of the mongoose populations in Portugal, using modern molecular genetic techniques, including a non-invasive genetic sampling approach. In this study, besides tissue, blood and hair samples collected from mongoose specimens resulting from capture-programmes, road-kills or hunting activities, faeces were also collected in order to be used as non-invasive source of genetic material. By combining molecular techniques with traditional ecological methodologies, this project also intends to identify trade-offs and bias between genetic and capture/tagging strategies in studies on the ecology of mongooses and of carnivores in general, and to propose guidelines for animal census and monitoring using faecal DNA analysis. Total DNA was extracted using different extraction protocols, aiming optimisation and/or depending upon the sample type. So far, Egyptian mongoose-specific primers that are likely to allow the analysis of short sequences amplified from faecal material or other degraded DNA source were designed through sequencing the entire mitochondrial DNA cytochrome *b* gene of 16 individuals. A microsatellite-genotyping procedure was tested and optimised using tissue samples with primers described for meerkats (*Suricata suricatta*) and for other carnivores. In the near future, faecal molecular analyses using these microsatellites will be developed.

9.49P

POPULATION GENETICS USING DEVELOPMENTAL GENES AS MARKERS: THE CASE OF THE PRE-GLACIAL ENDEMIC *RAMONDA MYCONI*

[1]F.X. Picó, [2]M. Möller, [1]N.J. Ouborg, [3]Q.C.B. Cronk,

[1]*University of Nijmegen, Toernooiveld 1, 6525 ED Nijmegen, The Netherlands*

[2]*Royal Botanic Garden, 20A Inverleith Row, Edinburgh EH3 5LR, United Kingdom*

[3]*UBC Botanical Garden, 6804 SW Marine Drive, Vancouver B.C., V6T 1Z4, Canada*

Population genetics describes the changes of frequencies of alleles and genotypes within and among populations across time and space. At the population level, genetic variation produces phenotypic variation that can be under selection in particular environments. Assuming that one of the most important statements in the developmental evolutionary theory is that variability in developmental genes drives evolutionary change, it becomes crucial to examine the extent of within- and between-population variation in those genes. Furthermore, it is becoming widely accepted that micro-mutations in genes included in developmental pathways may explain biological diversification. Based on this theoretical background, this communication presents results on the extent of within- and between-variation in the gene *Gcyc* in the long-lived herb *Ramonda myconi* (Gesneriaceae). *Gcyc* is a developmental gene (the homologue of CYCLOIDEA in Gesneriaceae) involved in the expression of floral morphology. Gesneriaceae is a tropical family of flowering plants with a few extant relict species in Europe. One of them is *Ramonda myconi* Rchb., a pre-glacial endemic plant occurring in NE Spain. Climatic conditions over the species' distribution area show great differences, ranging from sub-alpine in the north to Mediterranean in the south. A total of 20 plants from one northern and one southern population were sampled and *Gcyc* sequenced. Results showed a total of four single nucleotide polymorphisms (SNPs). All four SNPs were found in the southern population, whilst only one SNP was found in the northern population, suggesting a differential effect of glaciations in *R. myconi* populations. Three SNPs led to non-synonymous substitutions. *R. myconi* presents variation in floral morphology due to a 180° rotation in flower position, which could be attributed to changes in *Gcyc*. Further studies will focus on the extent of floral morph variation in wild populations and the link between variation in *Gcyc* and floral morphological traits.

9.50P

GENETIC DRIFT ERODES FITNESS IN NATURAL POPULATIONS OF AN AQUATIC SNAIL

[1]Mikael Puurtinen, [1]K. Emily Knott, [1]Susanna Suonpää, [2]Veijo Kaitala,

[1]*University of Jyväskylä, P.O.Box 35, 40014 Finland*

[2]*University of Helsinki, Finland*

Fixation and accumulation of mildly deleterious mutations by genetic drift may constitute a serious risk of extinction to small and isolated populations. We have studied eight natural populations of *Lymnaea stagnalis*, a hermaphroditic aquatic snail, and found strong evidence for fitness decrease as a consequence of small effective population size. We used microsatellite markers to infer self-fertilization rates and the past population sizes (allelic richness) of each of the populations. In the laboratory, we obtained estimates of two fitness components (fecundity and age at maturity) and also estimated inbreeding depression in hatching success. All populations were predominantly cross-fertilizing. Among populations, fecundity was positively ($r = .790$, $P = .020$) and age at maturity negatively ($r = -.944$, $P < .001$) correlated with allelic richness, demonstrating the negative effects of small effective population size to fitness. Frequency of highly detrimental alleles (measured as inbreeding depression in hatching success) was not correlated with allelic richness, as expected from efficient natural selection against alleles of large effect.

9.51P

RELATEDNESS OF ENDANGERED POPULATIONS OF CAPERCAILLIE (*TETRAO UROGALLUS*) ON LEK SITES IN THE SWISS AND FRENCH JURA.

Sébastien Regnaut, Luca Fumagalli

University of Lausanne, Lab. for conservation biology, inst. of Ecology. Bat Biol. CH-1008 Dorigny, Switzerland

In the Swiss Jura, few leks of Capercaillie remain, following the general trend of drastic decline of all European populations of this species. These populations are closely looked out for by naturalists and conservation associations. Our thorough study is based on non-invasive genetic sampling, i.e. feces sampled on and around lek sites, scoring 10 microsatellite loci. We address the question of the actual mating system, which has only been described by field observation. We studied relatedness and dispersal pattern on different leks. We found that males are more closely related to males from the same lek than to males displaying on other leks. This pattern was already described in other lekking galliformes (peacock, black grouse). We also found higher Fst values in males than in females, indicating a higher propensity to dispersal for the female, confirming many field observations. We will discuss evolutionary pendents and conservation implications.

9.52P

REPRODUCTIVE BARRIERS BETWEEN ECOTYPES OF A SNAIL HAVE SYMPATRIC ORIGINS AND HAVE EVOLVED BY PARALLEL EVOLUTION

[1]E. Rolán-Alvarez, [1]M. Carballo, [1]B. Fernández, [1]P. Moran, [1]J. Galindo, [1]A. Caballero, [2]R. Cruz, [3]E. Boulding, [4]K. Johannesson

[1]Departamento de Bioquímica, Genética e Inmunología, Facultad de Ciencias, Universidad de Vigo, 36200 Vigo, Spain

[2]Departamento de Biología Fundamental, Facultad de Biología, Universidad de Santiago de Compostela, 15706 Santiago, Spain

[3]Dept. of Zoology, University of Guelph, Guelph, ON N1G 2W1, Canada

[4]Dept. of Marine Ecology, Göteborg University, Tjärnö Marine Biological Laboratory, Strömstad, S 45296, Sweden

Theoretical models show that speciation is possible without an initial stage of physical isolation of populations, but we need more empirical observations from nature to test this hypothesis. Strong directional selection in each of two neighboring rocky shore microhabitats causes populations of a marine snail (*Littorina saxatilis*) to produce a large, thick-shelled ecotype in the upper intertidal zone and a small, thin-shelled ecotype in the lower intertidal. The ecotypes overlap and hybridize in a narrow mid-shore zone. Frequencies at allozyme, mtDNA and microsatellite loci indicate partial reproductive isolation between the ecotypes within shores (at maximum 40 m distance). However, these differences disappear when comparing neutral variation (mtDNA and microsatellites) between ecotypes from distant shores (samples from distances of >10 km). Such a pattern of genetic variation supports that the ecotypes as well as the reproductive barriers are being formed independently at each shore by parallel evolution and without physical isolation (non-allopatry), while this pattern is less compatible with a model based on allopatric ecotype formation, secondary overlap and introgression. Ecological data indicate that the reproductive barriers arise as byproducts of directional selection favoring different sizes of snails in upper and lower shore microhabitats. Speciation by ecological mechanisms are presumably much faster than speciation by the classical routes (genetic incompatibility generated over long periods of physical isolation). Parallel evolution of reproductive barriers indicates furthermore that reproductive barriers might evolve repeatedly under the right circumstances. While we have mainly been concerned about species extinctions and loss of genetic variation, we might as well be aware of the possibility to interact, on a human-relevant time-scale with processes that promote differentiation and even speciation. Thus knowledge about these processes has implications for management.

9.53P

MITOCHONDRIAL PHYLOGEOGRAPHY AND THE CONSERVATION OF THE RED KITE, *MILVUS MILVUS*

S. Roques

Dpt. Applied Biology, Estacion Biologica Donana (CSIC), Avda. Mª Luisa s/n, Sevilla 41013, Spain

Recent natural and anthropogenic disturbances have endangered many raptors species throughout Europe. The red kite (*Milvus milvus*) is distributed in the southwestern palaeartic region, with main populations confined in Central Europe. However, only a small number of breeding pairs remains at the extreme limit of its range. In order to measure and compare levels of genetic diversity among various geographic sites (south Spain, Balearic Islands, Italy, Germany and Switzerland), sequence variation of a 380 bps of the mitochondrial DNA control region was assessed in 100 red kite samples. Unexpectedly, we found an extremely low level of genetic diversity, with eight distinct haplotypes resolved, separated by low levels of genetic divergence. Highest haplotype diversity was found in Central European samples (Mean H=0.734), while Balearic samples showed very low values (Mean H=0.041). Fst estimates indicated high gene flow between Balearic islands and southern Spain, while higher genetic differences were found between southern Spain and Central Europe (Italy, Switzerland). We will discuss the low level of genetic variation in the control region of the red kite, as the probable result of successive bottlenecks and small population sizes. These results are important for the management of the species to provide guidelines for reintroduction projects.

9.54P

THE DOMINANCE OF THE HERBICIDE RESISTANCE COST IN SEVERAL *ARABIDOPSIS THALIANA* MUTANT LINES

F. Roux, J. Gasquez, X. Reboud

UMR BGA, 17 rue Sully, INRA BP86510, 21065 Dijon, France

The major obstacle to pest control programs has been the evolution of resistance toward xenobiotics for the last 40 years. The genetic component of the resistance fate depends on the selective advantage or disadvantage (cost) given by a resistance allele in the presence or absence of pesticides in the environment, as well as the dominance of this effects. While the dominance levels of the resistance trait are well studied, no study has been specially designed to measure the dominance of resistance cost. This is an important pursuit nonetheless because the spread and establishment of resistance genes may initially depend on the fitness of heterozygous individuals. Analysing both the morphological characters and simple fitness components, cost were studied for eight herbicide resistances using the plant model *Arabidopsis thaliana* . The use of allele-specific PCR to discriminate between heterozygous and homozygous resistant or sensitive plants allowed to analyse the dominance of the cost. Here, we demonstrated that a given resistance may be either recessive or dominant depending on the environment (untreated and treated areas). The origin of fitness cost, the relation to theoretical predictions of dominance or recessivity, the consequences of fitness cost and dominance of this cost in the absence of xenobiotics are discussed with regard to both genes properties and resistance management. Keywords: fitness impairment, dominance, resistance, management.

9.55P

GENE FLOW, SONG DIVERGENCE, AND BIRD SPECIATION.

[1]H. Slabbekoorn, [2]T. B. Smith,

[1]Behavioural Biology, Leiden University, Kaiserstraat 63, 2311 GP, Leiden, The Netherlands

[2] Center for Tropical Research, Institute of the Environment, UCLA, Los Angeles, Califormia, USA

Strong divergent selection in natural populations may lead to divergence in traits of ecological importance despite gene flow. Bird song is a sexual trait important in mate choice, and also known to be shaped by environmental selection. Therefore, habitat-dependent divergent selection may act simultaneously on traits for example related to morphology and a sexual trait like song. This can lead to an association between morphological and acoustic divergence, which may promote assortative mating and speciation. Song is a phenotypically plastic trait in many bird species that have to learn the acoustic details from conspecific tutors. Song plasticity may allow individuals to adjust to locally appropriate acoustic characteristics. This can lead to very rapid acoustic divergence among populations, potentially promoting reproductive divergence. On the other hand, acoustic flexibility likely improves reproductive chances for individuals switching habitats. This will obviously counteract reproductive divergence. I will address these issues with molecular and acoustic data from little greenbuls (*Andropadus virens*) in Cameroon and great tits (*Parus major*) in the Netherlands.

9.56P

GENETIC AND ECOLOGICAL DIVERSITY IN A CORAL REEF SEA ANEMONE (*CONDYLACTIS GIGANTEA*)

N. Stoletzki, B. Schierwater,

Beethovenstr 4, Hannover, Germany D-30449

Understanding the genetic origin and maintenance of biodiversity in the sea is crucial to the management of marine conservation efforts. Especially in the sea, speciation processes are still poorly understood. The tropical sea anemone *Condylactis gigantea* inhabits a broad spectrum of coral reef habitats and displays a variety of different phenotypes, for example in coloration of tentacle tips. At the coast of Discovery Bay, Jamaica, pink and green color morphs differ in their distribution. DNA sequence data (ITS1-5.8S-ITS2) was used to assess spatial genetic structure and to investigate whether ecophenotypic variation in color is coupled to genetic differentiation. Representatives of both color morphs were sampled at forereef and lagoon habitats about 5 km apart. Phylogenetic and population genetic analyses revealed two cryptic lineages of *Condylactis gigantea*, which do not correspond to the green and pink phenotypes in general. Because the lineages occur in sympatry with a dearth of intermediates, some reproductive isolation mechanism is indicated. *Condylactis gigantea* is gonochoric with a broadcasting mode of reproduction. Spawning has to be synchronized by a specific control mechanism or by environmental cues. This is where reproductive isolation mechanisms could come into play. Future work should test if barriers of synchronization are involved in allowing these closely related populations to remain isolated. Ecologically driven reproductive isolation combined with adaptations to divergent niches is a plausible explanation to cause genetic substructuring in sympatry. The two genetic lineages show adaptive differences. Distinct habitat requirements or preferences are indicated by their distribution and abundance. In the lagoon habitat, different color expression and differences in the production of UV absorbing substances have been found. This work supports the view that intrinsic barriers and local adaptation may lead to sympatric speciation and could account for much of marine diversity.

9.57P

A MULTI-LOCUS ANALYSIS OF VARIATION IN *ARABIDOPSIS*: COMPARISON BETWEEN THE OUTBREEDERS *ARABIDOPSIS LYRATA* AND *A. HALLERI*, AND THE INBREEDER *A. THALIANA*

[1]Barbara E. Stranger, [2]S. E. Ramos-Onsins, [1]M. Aguadé, [2]T. Mitchell-Olds

[1]*Universitat de Barcelona, Diagonal 645, Barcelona, Spain*

[2]*Max Planck Institut für chemische Ökologie, Winzerlaerstrasse 10, Jena, Germany*

Nucleotide variation in eight effectively unlinked genes was surveyed in species-wide samples of the closely related outbreeding species *Arabidopsis halleri* and *A. lyrata* ssp *petraea*, and in three of these genes in *A. lyrata* ssp *lyrata* and inbreeding *A. thaliana*. Significant genetic differentiation was more frequently observed in the patchily distributed *A. l. petraea* than in the more continuously distributed *A. halleri*. Average estimates of nucleotide variation were highest in *A. l. petraea* and lowest in *A. l. lyrata*, reflecting differences among species in effective population size. In general, the data support theoretical predictions that outcrossing species have higher variability than inbreeding species, with the exception of *A. l. lyrata*. Additional aspects of the data suggest further suggest that *A. lyrata* experienced a population bottleneck during its colonization of North America, and that this bottleneck substantially reduced within species variability.

9.58P

EVOLUTIONARY DYNAMICS OF INTRASPECIFIC COLOUR POLYMORPHISMS: INSIGHTS FROM DIFFERENT TAXA ON TWO CONTINENTS

Erik I. Svensson

Lund University, Department of Ecology, SE-223 62 Lund, Sweden

Intraspecific discrete phenotypes (morphs) have revealed many important population processes and can also provide cues to the mechanisms of speciation. Such polymorphisms are typically formed through the processes of disruptive and frequency-dependent selection, driven by the competition for essential resources, e.g. food or mates. Although the genetic basis of morphs is usually quite simple (e. g. one locus), they often differ in several morphological, physiological and behavioural traits. One important question is whether such morphs will become incipient species and evolve reproductive isolation between them, or whether they will continue to segregate within a single species as a balanced polymorphism. In the latter case, they may become involved in genetic cycles between generations driven by time-lagged negative frequency-dependent selection. I will illustrate these processes with field data from two polymorphic taxa (side-blotched lizards *Uta stansburiana* and blue-tailed damselfly *Ischnura elegans*) on two different continents (Europe and North America). I will also discuss the genetic and ecological mechanisms leading to formation of new species vs. a balanced polymorphism.

9.59P

LOCAL POPULATION STRUCTURE IN AN ENDANGERED PLANT SPECIES, *SILENE TATARICA*

[1]Niina Tero, [1]Jouni Aspi, [2]Pirkko Siikamäki

[1]*Department of Biology, P. O. Box 3000, 90014 University of Oulu, Finland*

[2]*Oulanka Biological Station, Liikasenvaarantie 134, 93999 Kuusamo, Finland*

Habitat fragmentation is widely regarded as a major threat to species diversity over the last century. Fragmentation may have several consequences on mating within populations. The main concern is increased inbreeding and accompanying inbreeding depression in small or isolated populations that might reduce their long-term viability and conservation value. The accurate characterization of plant mating system is essential for understanding of the intensity and evolutionary consequences of factors affecting individual reproductive success. *Silene tatarica* (L.) Pers. (Caryophylleaceae) is an endangered, perennial plant species growing along periodically disturbed riverbanks of two rivers in northern Finland. Earlier study using AFLP-markers has revealed that the overall pattern of genetic variation within and between subpopulations in *S. tatarica* obeys a 'classical' metapopulation model. In this study we extended our AFLP-analysis to describe the microspatial structure of *S. tatarica* in a river island population with 38 plants. Spatial autocorrelation analysis and clustering of individuals on the basis of genetical similarity revealed clear spatial genetic structure in *S. tatarica*, probably due to limited seed dispersal. We collected seeds from all naturally pollinated plants in the population, and germinated them under laboratory conditions. We estimated the AFLP-genotypes of 214 offspring from 19 mothers. Paternity analysis revealed that most families were multiply sired, and that there was differential male success of flowering individuals within the population. The population was predominantly outcrossing with minimal amount (< 1%) of selfcrossing. Pollen moved from 0 m to 47 m, and the mean pollen movement (24 m) was significantly longer than the mean distance between the individuals. The results suggested that despite of free pollen movement across population, restricted seed dispersal may maintain local genetic structure in *S. tatarica.*

9.60P

GENETIC POPULATION STRUCTURE OF THE INQUILINE PARASITE ANT *PLAGIOLEPIS XENE*

[1]Kalevi Trontti, [2]Serge Aron, [1]Liselotte Sundström

[1]*University of Helsinki, Department of Ecology and Systematics, P.O. Box 65 (Viikinkaari 1), 00014 Helsinki, Finland*

[2]*Université libre de Bruxelles, Faculté des sciences, Laboratoire de biologie animale et cellulaire, CP 160/12 (avenue F.D. Roosevelt 50), B-1050 Bruxelles, Belgique*

Socially parasitic ants have evolved to exploit the worker force of another ant species in their own reproductive interests. In the extreme case of permanent inquilinism, the social parasite has completely lost the worker caste and the entire life cycle of the parasite takes place within the host colony. Such inquilines usually exploit only one host species, as the intrusion into a host colony entails mimicking the chemical identity code of the host. Inquiline species typically also have strongly curtailed nuptial flights and reduced dispersal. Consequently the colonisation of new patches as well as gene flow between populations is impeded with inbreeding as a common consequence. Indeed, many inquiline parasites are rare or declining, which calls for studies on their reproductive biology. To date very few studies have analysed the genetic structure of social parasites and sympatric vs. allopatric populations of their host species. We analysed the genetic population structure in the inquiline parasite ant *Plagiolepis xene* and its host species *P. pygmaea* with 8 and 7 microsatellite loci, respectively. We found that the inquiline populations are truly fragmented as all three geographically separate study locations were genetically very different.

9.61P

GEOGRAPHICAL POPULATION STRUCTURE REVEALED BY MTDNA SEQUENCES IN THE NW IBERIAN ENDEMIC BUTTERFLY *EREBIA PALARICA*: DEMOGRAPHY ON A FINE SPATIAL SCALE.

[1,2]Marta Vila, [2]J. Ramón Vidal-Romaní, [1]Mats Björklund

[1]*Department of Animal Ecology, EBC, Uppsala University, Norbyvägen 18D SE-752 36 Uppsala, Sweden*

[2]*IUX-Faculty of Sciences, University of A Coruna, Campus da Zapateira s/n E-15071 A Coruna, Galicia, Spain.*

Many *Erebia* species from southern-central Europe are considered as glacial relicts due to their high altitude distribution areas. Some of them show plasticity in their life-cycle length, being annual or biennual depending on the latitude.

To test for significant differences between years and among close geographical locations - average distance 46 km- in *Erebia palarica*, we sequenced 356 bp of the mitochondrial Control Region and 786 bp of the COI in twenty individuals from 1998 and twenty from 1999 from a same locality (A). We surveyed the degree of differentiation putatively attributed to allochrony and the degree of divergence compared to two other separated populations (C, Q; n = 20 each) from 1999.

Twenty different haplotypes were obtained. No allochronic differentiation was found, but an AMOVA showed substantial divergence among locations. Combining both markers resulted in a highly significant F_{st} of 0.19. All populations showed signs of a recent bottleneck regardless of the marker used. The haplotype distribution across populations was highly non-random and the variance in the frequences of haplotypes was always much larger than expected assuming a stable population. The degree of differentiation and a test of possible bottlenecks were concordant, and this is true to a lesser extent also for the expansion test. The null hypothesis of no geographical association was significantly rejected by a nested contingency analysis in two out of three categories. Past fragmentation for populations (A) and (C) was inferred by a nested clade analysis. Fragmentation was also indicated for populations (C) and (Q) based on coalescence simulations. Migration was clearly asymmetric as resulted from maximum likelihood estimations, sending population (C) most migrants to the other two. Population (A) showed the highest effective population size.

The sequence variability of this endemic species is very low when compared to congeneric sympatric species

9.62P

GENE FLOW, FISHERIES MANAGEMENT AND CONSERVATION OF DOVER SOLE

[1]Filip A.M.J. Volckaert, [1]B. Hellemans, [2]P. Bossier

[1]*Katholieke Universiteit Leuven, Laboratory of Aquatic Ecology, Ch. de Bériotstraat 32, B-3000 Leuven, Belgium*

[2]*Department of Fisheries, Ministry of the Flemish Community, Ankerstraat 2, B-8400 Oostende, Belgium and University of Ghent, Laboratory of Aquaculture and Artemia Reference Centre, Rozier 44, B-9000 Gent, Belgium*

Many commercial marine fish stocks are over-fished and hence suffer imminent population collapse. The question arises to what degree this affects structure, recurrent gene flow and population characteristics. Twenty samples of each about 30 adult Dover sole (*Solea solea*, Teleostei) were collected along the shores of the Northeastern Atlantic Ocean and the Mediterranean Sea. They were genotyped at six microsatellite loci and at the ND5/6 locus by Single Strand Conformational Polymorphism. Typically for many marine organisms, haplotype and microsatellite diversity were high; the highest haplotype diversity was observed in the western Mediterranean Sea. Genetic differences between populations were limited (microsatellite multi-locus GST = 0.10), but they show a pattern of isolation-by-distance. It erases most of the genetic discreteness of neighbouring populations but seems to maintain the phenotypic differentiation among stocks. The impact of fishing on cohort structure and effective population size suggests the need for urgent conservation measures.

9.63P

DIFFERENTIAL GENE EXCHANGE IN *LITTORINA SAXATILIS*

H. M. Wood, R. K. Butlin, J. W. Grahame

School of Biology, The University of Leeds, Leeds LS2 9JT, U.K.

This study aims to investigate a natural model to document differential gene exchange, to test hypotheses about the origins of the differentiation between morphs, and to measure the extent of the regions of differentiation. In the rough periwinkle *Littorina saxatilis* we find that two forms are observed widely in Britain, **H**igh and **M**id-shore, differing in a number of ways, most noticeably shell morphology and habitat. Along a shore transect a steep cline is observed between the two. AFLP analysis has produced 306 polymorphic loci. Of these, 15 are differentiated between the two forms and show a cline matching that of morphology. The rest are evenly spread up and down the shore with a larger (geographical) scale of variation. This suggests that the minority of loci are influenced by selection impeding gene exchange, while the majority are free to drift. We may be observing that critical intermediate stage of evolutionary divergence leading to speciation, not complete until there is a barrier to gene exchange across the whole genome.

We will probe a BAC library from *Littorina saxatilis* to identify clones containing the AFLP markers known to mark differentiated and undifferentiated regions. Shotgun sequencing of candidate BACs will allow genes likely to be involved in differentiation between morphs to be sequenced in a number of individuals; we hope then to test hypotheses for the origin of differentiation by analysis of sequence diversity and divergence and by comparison to coalescent simulations. We also aim to establish the size of genomic regions of differentiation.

9.64P

PATTERNS OF GENETIC VARIATION IN MARGINAL POPULATIONS OF *IRIS APHYLLA* IN POLAND.

Ada Wróblewska, Emilia Brzosko

University of Bialystok, Institute of Biology, Swierkowa 20B, 15-950 Bialystok, Poland

Reconstruction of the colonization of Europe by steppe plants and detection of the patterns of genetic diversity, particularly in marginal populations, are still in infancy and discussed. Therefore, *Iris aphylla* was chosen for the present study due to its steppe character, geographical as well historical distribution, which make possible to investigate marginal and isolated populations. Genetic analysis based on RAPD markers revealed relatively high genetic diversity within 7 Polish populations (Shannon's indices 0.11-0.23). Analyses of AMOVA with distances among 210 individuals showed high value (22%) of among-populations variability, indicating population differentiation as expected for an outcrossing, animal-pollinated species and also polyploid species as *Iris aphylla.* The results of AMOVA together with the lack of correlation between pairwise F_{ST} values and geographic distances among populations (Mantel test r=-0.29, p=0.70) implicated that habitat differentiation could be more important that the large-scale geographic differentiation to account for variation in the populations. Two-dimensional PCA of all individuals showed three genetically distinct population groups, one from north and south-eastern and two others from south Poland. We hypothesized that the present populations of *Iris aphylla* may originate from different source populations from refugia and infrequent gene flow among them (Nm=0.94) may contribute that each population evolved independently.

9.65P

GEOGRAPHIC VARIATION IN ANT HOST USE IN *MACULINEA* BUTTERFLIES - A MOLECULAR APPROACH

Inga Zeisset, Jon Ebsen, Ian R. Wynne, David R. Nash

University of Copenhagen, Universitetsparken 15, 2100 Copenhagen

The endangered butterflies of the genus *Maculinea* are unusual among the lycaenids in being parasites of *Myrmica* ant colonies. The adult butterflies lay eggs on specific food plants on which the first three larval instars feed. Once the fourth instar is reached, the larva leaves the plant, drops to the ground, and is "adopted" by an ant colony, where the caterpillar becomes a parasite of the ants. *Maculinea alcon* is one of the five currently recognized *Maculinea* species found in Europe. It is unusual within this genus in that it parasitizes the nests of several different *Myrmica* species (*M. rubra, M. ruginodis* and *M. scabrinodis*). However, host use varies geographically throughout Europe, and there is some evidence for local adaptation as well as large scale geographical host preferences.

The degree to which local host ant use is influenced by, for example host availability, local host adaptations, metapopulation processes and phylogeography (of host and parasite) is largely unknown. Shedding light on these factors will be of great importance for *Maculinea* conservation and management and here we present preliminary findings of on-going studies employing molecular markers to investigate them.

Symposium 10

Experimental microbial evolution: the roles of sex, recombination and mutation

Organisers: Santiago F. Elena, J. Arjan G. M. de Visser and Graham Bell

Roger Stevens Lecture Theatre 22

09.50 – 10.20	**Bell, G.** Experimental sexual selection in *Chlamydomonas*
10.20 – 11.00	**Coffee**
11.00 – 11.30	**Taddei, F.** Sources of genetic and phenotypic variability
11.30 – 12.00	**Bohannan, B. J. M.** Using microbial model systems to explore spatially-explicit evolutionary theory
12.00 – 12.20	**Korona, R.** When defects cannot be masked: a case study with deleterious mutations in yeast
12.20 – 12.40	**Schoustra, S.** Experimental evolution in *Aspergillus nidulans*: reducing the cost of resistance
12.40 – 14.00	**Lunch**
14.00 – 14.20	**Velicer G.** Evolution of cooperation in a social bacterium
14.20 – 14.40	**de Visser J. A. G. M.** Experimental rejection of non-transitive interactions as cause of declining rate of evolution in *E. coli*
14.40 – 15.00	**Hughes, D.** Evolution of fluoroquinolone resistance in urinary tract infection *E. coli*
15.00 – 15. 20	**Collins, S.** Evolutionary Response to Rising Levels of Carbon Dioxide in *Chlamydomonas reinhardtii*
15.20 – 16.00	**Tea**
16.00 – 16.20	**Elena, S. F.** The experimental evolution of gene regulation and expression: the case of the *tet*AR operon
16.20 – 16.40	**Buckling, A.** Specialization constrains diversification of *Pseudomonas fluorescens*
16.40 – 17. 00	**Spiers, A.** Multiple evolution to a single niche: comparative analysis of the *Pseudomonas fluorescens* wrinkly spreaders
17.00 – 17.20	**Bell, G.** Closing remarks.

Invited talks

10.1

EXPERIMENTAL SEXUAL SELECTION IN *CHLAMYDOMONAS*

Graham Bell

McGill University, Montreal, Canada

Sexual selection is more difficult than natural selection to study in the laboratory, and relatively few extensive experiments have been conducted. Evolutionary experiments, moreover, have often given rise to ecologically distinct lines, but have been much less successful in creating sexually isolated lines. Selection in environments that offer different conditions both for growth and for mating might cause both vegetative and sexual divergence through concerted natural and sexual selection. I shall report progress in a long-term sexual selection experiment using *Chlamydomonas*, where the genetic basis of sex and gender is simple and evolves rapidly. We have maintained lines that both grow and mate only in liquid or only on solid medium for about 100 sexual cycles comprising about 1000 asexual cycles. I shall describe the changes caused by sexual selection in the rapidity of mating, the system of gender and the extent of sexual isolation.

10.2

SOURCES OF GENETIC AND PHENOTYPIC VARIABILITY

Francois Taddei

Genetique Moleculaire Evolutive et Medicale, INSERM U571, Faculte de Medecine "Necker - Enfants Malades"

Universite Rene Descartes-Paris V, 2eme etage, 156 Rue de Vaugirard, 75730 Paris Cedex 15, France

The availability of hundred of genomes allow us to learn rapidly about genomic differences between micro-organisms. Comparative genomics shows that horizontal gene transfer, mutations and rearrangements are frequent events in most species. The molecular mechanisms for these events have been described in laboratory experiments and sometimes even under "natural conditions". Beside, when put in different environments, a given bacterial genome shows drastic change in its profile of expression (as evidenced by transcriptomic or proteomic experiments). Thus, clearly genetic differences and variation in environmental conditions lead to phenotypic variability (ie. as text book say genotype X environment = phenotype). However, there might be other sources of phenotypic variability as experiments show that even with a given genome in a given environment one observes phenotypic variability. Even if this was recognized already in the 50's, the causes and consequences of this other source of phenotypic variability remain to be described presumably by developing new interdisciplinary tools.

10.3

USING MICROBIAL MODEL SYSTEMS TO EXPLORE SPATIALLY-EXPLICIT EVOLUTIONARY THEORY

Brendan J. M. Bohannan

Stanford University, 371 Serra Mall, Stanford, CA 94305 USA

Increasingly, ecologists and evolutionary biologists are turning to individual-based, spatially-explicit approaches to modeling ecological and evolutionary processes. We have developed several microbial model systems for exploring the predictions of such theory. For example, we have been studying a model community consisting of three populations of the bacterium *Escherichia coli*: 1) a toxin producer, which is immune to the action of the toxin it produces, 2) a strain sensitive to the toxin, and 3) a strain resistant to the toxin. These three populations satisfy a non-transitive "rock-paper-scissors" relationship, where population 1 kills 2, 2 outgrows 3, and 3 outgrows 1. Spatially-explicit computer simulations of this community predict that all three types will coexist if dispersal and interaction among types occurs locally. In contrast, one strain is predicted to exclude the others if dispersal and interactions occur more widely. Furthermore, these models make several counter-intuitive predictions regarding the evolution of this community; for example, selection is predicted to favour slower population growth rates and minimal growth rate differences among the populations when dispersal and interaction are local. These predictions were tested empirically by propagating the model community via replica plating (allowing interaction and dispersal on a local spatial scale only), mixed flask culture (allowing interaction and dispersal on a large scale), and replica plating with regular mixing (allowing an intermediate scale of dispersal and interaction). We observed that all three types could persist only when the scale of interaction and dispersal was local, as the models predicted. Over moderate evolutionary time scales (<150 generations), we observed changes in relative competitive fitness coupled with a breakdown in coexistence of the populations, as the models predicted. However, over longer time scales (>150 generations) two of the three populations were observed to coexist, in contrast to the model predictions.

Contributed talks

10.4

WHEN DEFECTS CAN NOT BE MASKED: A CASE STUDY WITH DELETERIOUS MUTATIONS IN YEAST

Ryszard Korona

Institute of Environmental Sciences, Jagiellonian University, 30-387 Krakow, Poland

Mutations in haploid populations of budding yeast show very different fitness effects, ranging from lethal to nearly neutral. This variety of effects is greatly reduced when the same mutations are in heterozygous loci of diploid strains where almost all of them become either slightly deleterious or virtually neutral. Thus, heterozygosity would lead to accumulation of defected genes in populations. It is possible; however, that natural selection can be more efficient under stressful conditions when masking by wild-type alleles appears to be weaker. Several explanations of this phenomenon are possible. Harmful effects can become generally stronger and therefore more visible in heterozygous loci even if their relative dominance remains unchanged. Alternatively, dominance of deleterious mutations may be higher under stress. The wealth of knowledge and variety of tools accessible for yeast make it an especially suitable model for studies where imported questions of population genetics can be linked to cellular processes.

10.5

EXPERIMENTAL EVOLUTION IN THE FILAMENTOUS FUNGUS *ASPERGILLUS NIDULANS;* REDUCING THE COST OF RESISTANCE

S. Schoustra, F. Debets, R. F. Hoekstra

Laboratory of Genetics, Wageningen University, Wageningen 6703 BD, The Netherlands

In my talk I will discuss the possibilities and special features of the filamentous fungus *Aspergillus nidulans* as model organism for experimental evolution. An *A. nidulans* colony expands radially from the point of inoculation, creating a spatially structured mycelium. This makes the number of effective cell cycles in the growing front of the colony remarkably high, up to 112 cell cycles in one week at 37°C. Linear growth rate (LGR) appears to be a suitable and highly reproducible fitness measure. Neutral and beneficial mutations can form pure sectors in expanding colonies. The fungus has an asexual and a sexual reproductive system and can grow vegetatively as a haploid and a diploid.

I will present the results of an evolution experiment (>3000 cell cycles) in which we show that a fungicide resistant *A. nidulans* strain with a fitness burden can rapidly restore its fitness and even reach a higher fitness than the original sensitive strain. When comparing compensatory evolution in haploids and diploids, it appears that in our setup haploids initially compensate faster for the cost of resistance than diploids. Diploids however appear to eventually reach a higher fitness than haploids. Finally, I will show the results of sexual crosses of evolved lines with their ancestors and with other evolved lines in order to try to achieve even higher fitness by recombination and to separate the mutations involved.

10.6

EVOLUTION OF COOPERATION IN A SOCIAL BACTERIUM

Gregory Velicer

Department of Evolutionary Biology, Max-Planck Institute for Developmental Biology, Spemannstrasse 35, Tübingen, Germany

Microorganisms offer unique potential to directly study the evolution of cooperative interactions. We have observed the evolution of novel forms of cooperative behaviour in experimental populations of the bacterium *Myxococcus xanthus*. Natural isolates of *M. xanthus* exhibit socially-dependent swarming across soft surfaces utilizing a system known as 'S-motility' that requires the presence of extracellular type IV pili. In lineages of *M. xanthus* unable to make pili due to a defined genetic deletion, a novel basis for cooperative swarming evolved. Evolved cooperative swarming is largely mediated by enhanced production of an extracellular fibril matrix that binds cells together. Though costly to individuals, evolved fibril production greatly enhances population expansion in groups of inter-connected cells. These results indicate that bacteria can readily evolve increased degrees of cooperative interaction.

10.7

EXPERIMENTAL REJECTION OF NON-TRANSITIVE INTERACTIONS AS CAUSE FOR DECLINING RATE OF ADAPTATION

[1]**J. A. G. M. de Visser**, [2]R. E. Lenski

[1]*Laboratory of Genetics, Wageningen University, Wageningen 6703 BD, The Netherlands*

[2]*Michigan State University, Dept. Microbiology and Molecular Genetics, East Lansing MI 48824, USA*

Experimental populations of *Escherichia coli* have evolved for 20,000 generations in a uniform environment. Their rate of improvement, as measured in competitions with the ancestor in that environment, has declined substantially over this period. This deceleration has been interpreted as the bacteria approaching a peak or plateau in a fitness landscape. Alternatively, this deceleration might be caused by non-transitive competitive interactions, in particular such that the measured advantage of later genotypes relative to earlier ones would be greater if they competed directly. To distinguish these two hypotheses, we performed a large set of competitions using one of the evolved lines. Twenty-one samples obtained at 1,000-generation intervals each competed against five genetically marked clones isolated at 5,000-generation intervals, with three-fold replication. The pattern of relative fitness values for these 315 pairwise competitions was compared with expectations under transitive and non-transitive models, the latter structured to produce the observed deceleration in fitness relative to the ancestor. In general, the relative fitness of later and earlier generations measured by direct competition agrees well with the fitness inferred from separately competing each against the ancestor. These data thus support the transitive model. Non-transitive competitive interactions were not a major feature of evolution in this population. Instead, the pronounced deceleration in its rate of fitness improvement indicates that the population early on incorporated most of those mutations that provided the greatest gains, and subsequently relied on beneficial mutations that were fewer in number, smaller in effect, or both.

10.8

EVOLUTION OF FLUOROQUINOLONE RESISTANCE IN URINARY TRACT INFECTION *E. COLI*

Diarmaid Hughes, Patricia Komp Lindgren, Linda Marcusson, Åsa Karlsson

Department of Cell and Molecular Biology (Microbiology Programme), Box 596, The Biomedical Center, Uppsala University, S-751 24 Uppsala, Sweden

Escherichia coli is the most common causative agent of urinary tract infections. Treatment with fluoroquinolones antibiotics such as Norfloxacin and Ciprofloxacin is very effective but resistance is increasing. Resistance to fluoroquinolones in *E. coli* arises as a result of chromosomal mutations in several different genes. These include genes for proteins targeted by fluoroquinolones such as DNA gyrase (*gyrA* and *gyrB*) and Topoisomerase IV (*parC* and *parE*), and genes involved in antibiotic efflux (*marOR* and *acr*). In addition alterations in the outer membrane proteins OmpF and OmpC have been implicated in fluoroquinolone resistance. Single mutations in most of these genes result in low level resistance whereas medium and high level resistance is typically associated with multiple mutations involving several of the genes above. The multitude of genes involved, each individually capable of mutating to increase the level of resistance, means that the evolution of resistance is potentially very complex. A question we are interested in is whether there are preferred pathways of evolution, in particular in the clinical strains. A closely related question is whether there are biological costs associated with resistance mutations, and in particular with the accumulation of the multiple mutations associated with high level resistance. Our experimental evidence suggests that, as might be expected, the accumulation of mutations *in vitro* is associated with large biological costs. However, our collection of clinical strains, including strains with high level resistance and multiple mutations, reveals no obvious correlation with biological costs for these mutations. Alternative models include the presence of cost-compensating mutations, or the selection of particular cost-free combinations, in the clinical isolates. We will discuss the use of genetic re-constructions and fitness assays to assess the relevance of these models.

10.9

EVOLUTIONARY RESPONSE TO RISING LEVELS OF CARBON DIOXIDE IN *CHLAMYDOMONAS REINHARDTII*

Sinead Collins, Graham Bell

McGill University, 1205 Ave Dr.Penfield, Montreal H3A 1B1, Canada

One of the important environmental changes that will occur over the next hundred years is a rapid increase in atmospheric carbon dioxide levels, yet little experimental data exists which details the evolutionary responses that plants are likely to have to this change. In order to test the long-term effect of increased carbon dioxide on microalgae, replicate lines of *Chlamydomonas reinhardtii* were selected for 1000 generations at increasing concentrations of carbon dioxide. Changes in fitness and the underlying basis for adaptation are discussed in terms of changes seen in the ability to concentrate and fix inorganic carbon.

10.10

THE EXPERIMENTAL EVOLUTION OF GENE REGULATION AND EXPRESSION: THE CASE OF *TET*AR

[1]**S. F. Elena**, [2]R. E. Lenski

[1]*Instituto de Biología Molecular y Celular de Plantas, CSIC, Avda. de los naranjos s/n, 46022 València, Spain*

[2]*Department of Microbiology and Molecular Genetics and Center for Microbial Ecology, Michigan State University, East Lansing MI 48824, USA*

Our goal was to analyze the specificity of adaptive changes that happen, under different environments, in a set of related host-plasmid systems. We started with a single host, *E. coli* B, and five plasmids encoding resistance to tetracycline. These plasmids had one of five engineered versions of the *tet*AR operon that differed in the mechanism of regulation (constitutive or inducible) and the level of gene expression (low, medium or, high). Each host-plasmid system evolved for 1,000 generations in four different environments that varied in the concentration of tetracycline or the periodicity at which it was added. At the end, we analyzed both the phenotype (fitness) and the genotype (sequencing regulatory elements of the *tet*AR operon). We sought to answer the following questions: Are the evolved solutions, at phenotypic and genotypic levels, the same for a given environment? Alternatively, for a given plasmid, were the solutions identical independent of the selective environment? In other words, were phenotypic and genotypic changes convergent or, by contrast, were outcomes dependent on the interaction between the particular plasmid and environment? In a further step, we explored (so far only at the phenotypic level) the coevolution between plasmid and chromosomal genes. The goal of this set of experiments was to elucidate whether changes in the chromosome were also selected and whether the effects of chromosomal mutations were specific to the partner plasmid or, by contrast, had a general beneficial effect.

10.11

SPECIALISATION CONSTRAINS DIVERSIFICATION OF *PSEUDOMONAS FLUORESCENS*

Angus Buckling

Department of Biology and Biochemistry, University of Bath, BA2 7AY, UK

Adaptive landscape models of evolution make the simple prediction that adaptation should limit a population's ability to diversify. We tested this using populations of the common plant colonising bacterium *Pseudomonas fluorescens*, which rapidly evolves into niche specialist genotypes in spatially structured environments. We allowed populations to diversify, randomly isolated genotypes, which were in turn allowed to diversify. We found a negative relationship between time spent evolving and ability to diversify, implying that the nearer an adaptive peak, the less available genotypic space. When the adaptive landscape was changed, by allowing genotypes to diversify in a novel media, no relationship was found between time spent evolving (in the original environment) and ability to diversify. These results suggest that in addition to reduced phenotypic plasticity, specialists are likely to show reduced genetic plasticity.

10.12

MULTIPLE EVOLUTION TO A SINGLE NICHE: COMPARATIVE ANALYSIS OF THE *P. FLUORESCENS* WRINKLY SPREADERS

A. Spiers, R. Kassen, C. Knight, P. Rainey

Bacterial Molecular Biology & Adaptation, Department of Plant Sciences, University of Oxford, United Kingdom

Department of Biology, University of Ottawa, Canada

School of Biological Sciences, University of Auckland, New Zealand

Wrinkly Spreaders (WS) are a class of novel mutants of the *bacterium Pseudomonas fluorescens* SBW25, capable of colonising the air-liquid interface in broth microcosms. Molecular analysis of one particular isolate has demonstrated that the ability to colonise this new environmental niche depends on enhanced bacterial attachment and the expression of cellulose as the matrix component of the biofilm. We have identified a single nucleotide change which is sufficient to convert the ancestral non-biofilm forming SBW25 strain into a wrinkly spreader. The mutation is in the coding region of the methyl esterase *wsp*F, part of the Wsp chemosensory system which serves to control both attachment and cellulose expression. Of a further 25 independently-evolved WS isolates, 12 were found to contain a variety of *wsp*F mutations. By mapping these onto the crystal structure of the highly similar CheB protein, and correlation with published structure-function analyses of this conserved group of enzymes, we were able to predict the likely effect of each mutation on WspF enzymatic activity. We were then able to investigate the relationship between the predicted activity of a key regulatory system capable, of directing a major shift of colonisation between ecological niches, with specific measurements of biofilm development and the fitness values of each WS genotype.

Posters

10.13P

MOLECULAR EVOLUTION AND TAXONOMIC RELATIONSHIPS IN THE FAMILY BROMOVIRIDAE BASED ON RNA-3 CODING GENES

Francisco M. Codoñer, José M. Cuevas, Jesús A. Sánchez-Navarro, V. Pallás & Santiago F. Elena

Instituto de Biología Molecular y Celular de Plantas, CSIC, Avda. de los naranjos s/n, 46022 Valencia, Spain.

Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Universitat de València, P.O.Box 22085, 46071 València, Spain

We have carried out a phylogenetic study of the evolution of the RNA-3 coding genes from members of the family Bromoviridae. Using maximum likelihood methods, we have inferred the patterns of molecular evolution responsible for the diversification of this family of plant viruses. The results indicate that the evolution of the different members of this family took place by a very complex pattern. First, we have detected heterogeneity in the mode and tempo of molecular evolution among each gene in the RNA-3, being the rates and patterns of amino acid substitution different for each one. Second, our analysis suggests that the commonly accepted assumption of a molecular clock does not hold, since different lineages evolved at different rates. Finally, three major features can be drawn from the phylogenetic studies that would modify the present status of the family Bromoviridae: (i) *Pelargonium zonate* spot virus (PZSV) is considered to be a new member of the Bromoviridae being the type member of a new genus that we propose to name *Pelarvirus*; (ii) Alfalfa mosaic virus (AMV) behaves as a true *Ilarvirus* instead of constituting a different genus and (iii) Ilarviruses are divided into five subgroups that can be extended to six, reflecting a common phylogeny of their RNA-3 rather than into seven subgroups based on their antigenic differences.

10.14P

A POLYMORPHISM FOR THE MUTATION RATE

I. Gordo, A. Marques, F. Dionisio

Institute Gulbenkian of Science, Oeiras, Portugal

Mutation is the ultimate source of genetic variation. But since the majority of mutations affecting fitness are deleterious, organisms have developed complex systems to minimize their mutation rate. Nevertheless high mutation rates are observed in pathogenic and commensal bacterial populations. Moreover, the spontaneous appearance of mutator clones (bacteria with an abnormally high mutation rate) has been observed in populations adapting to new environments. While bacteria with higher mutation rates can spread by being able to produce a higher number of adaptive mutations, they also pay a cost for producing a higher number of deleterious mutations. In experimental populations of *Escherichia coli*, we address the cost of high mutation rates. We find that, despite this cost, mutators can be maintained at a stable low frequency in populations by frequency-dependent selection. The resulting polymorphism for mutation rates provides a source of potentially rapid adapting clones, with a small load for the population as a whole. These results may be important to the understanding of evolution of mutators, pathogenic bacteria and certain types of cancers.

10.15P

EXPERIMENTAL EVOLUTION IN SPATIALLY-STRUCTURED ENVIRONMENTS

M. Habets, D. E. Rozen, J. A. G. M. de Visser, R. F. Hoekstra

Laboratory of Genetics, Wageningen University, Wageningen 6703 BD, The Netherlands

Spatial structure is thought to be an important factor influencing the emergence of genetic diversity. Different aspects of spatial structure may increase the opportunities for adaptation. First, as spatial structure often introduces environmental heterogeneity, more ecological niches may be available and competition can lead to genetic diversification. A second aspect of spatial structure is the localization of interactions, which may facilitate co-evolutionary interactions that allow co-existence (e.g. by cross feeding). Third, spatial structure leads to the fragmentation of the population into many small, relatively independent populations. Because of the greater role of genetic drift in such fragmented populations, the direction of adaptation is likely to be more contingent. Depending on the adaptive landscape, the variance of fitness and the maximum fitness among clones may be higher in a fragmented population, even though mean fitness is lower.

While the roles of the different aspects of spatial structure on the emergence of genetic diversity have been well considered from a theoretical standpoint, experimental evidence is limited. Here, we experimentally address the effects of fragmentation, the localization of interactions and environmental heterogeneity on the emergence of genetic diversity in asexual populations of *E. coli.*

10.16P

COEVOLUTION OF RESOURCE COMPETITORS

[1]Bas W. Ibelings, [1]Arnout De Bruin, [2]J. Arjan G. M. De Visser, [3]Jef Huisman, [1]Ellen Van Donk

[1]*Netherlands Institute of Ecology, Centre for Limnology, Rijksstraatweg 6, 3631 AC Nieuwersluis, The Netherlands*

[2]*Laboratory of Genetics, Wageningen University, Arboretumlaan 4, 6703 BD Wageningen, The Netherlands*

[3]*University of Amsterdam, Aquatic Microbiology, Institute for Biodiversity and Ecosystem Dynamics, Nieuwe Achtergracht 127, 1018 WS Amsterdam, The Netherlands*

The Red Queen hypothesis describes coevolution, the reciprocal adaptive genetic changes within populations of interacting species. We are testing the Red Queen's central prediction, that of accelerated evolution under strong biological interactions. We have chosen resource competition between the unicellular green alga *Chlamydomonas* and the cyanobacterium *Synechocystis* as the biological interaction driving coevolution. By comparing the rate of evolution during coevolutionary adaptation, to controls where coevolution is minimized the Red Queen hypothesis can be (dis)proved. Evolution is allowed for >1000 generations by serial transfer of the organisms in N-limited batch cultures. In controls the organisms are grown in the absence of a competitor. This would however still permit clonal interference in which clones carrying different beneficial mutations compete with each other. In a second type of controls one of the two competitors is repeatedly replaced by the ancestral strain, taken from the freezer, disallowing coevolution in both. The evolution of fitness - as the most important phenotypic trait - is assayed in a direct head to head competition between ancestor and evolved strains. Both competitors have been fully sequenced enabling a genomics approach to the study of molecular evolution. DNA microarrays are used to screen the evolving populations of both species for significant changes in gene expression. Genes that alter their expression are the first (but not the only) candidates to be involved in the coevolutionary adaptation. These genes will be sequenced at regular intervals to look for mutations. On basis of short generation times and a large effective population size of the organisms involved, plus an enhanced value of s (the fitness advantage of a beneficial mutation) under coevolutionary adaptation we expect some 50 adaptive sweeps during 1000 generations of experimental coevolution.

10.17P

DELETERIOUS MUTATIONS AND MOLECULAR CHAPERONES IN THE BUDDING YEAST

Joanna Kluz, Ryszard Korona

Institute of Environmental Sciences, Jagiellonian University, 30-387 Krakow, Poland

Natural selection is constantly purging populations of spontaneously arising deleterious mutations. This process is probably especially efficient under stressful conditions where masking by wild-type alleles in heterozygous loci is weaker. One possible explanation is that many mutated, and thus potentially misfolded, proteins can be effectively maintained in a good shape by a special class of proteins, the molecular chaperones, but only under non-stressful conditions. Under stress, the tendency to misfold is greater both in case of the mutated and numerous other non-mutated polypeptides. The chaperones become overloaded and can not mask the harmful effects of mutations. This hypothesis was confirmed in our studies of the budding yeast where mutations were accumulated in strains with a weakened chaperoning system and then exposed to stressful environments.

10.18P

EXPERIMENTAL SPECIALIZATION OF MICROSPORIDIAN PARASITES TO ISOFEMALE LINES OF THEIR MOSQUITO HOST

Mathieu Legros, Jacob C. Koella

Lab. Parasitologie Evolutive, 7 quai St Bernard -- CC237, 75252 Paris Cedex 05, France

In order to investigate the process of specialization of parasite on their hosts (and the trade-offs associated with the specialization), we are using an experimental evolution approach with the mosquito *Aedes aegypti* and its microsporidian parasite *Brachiola algerae*. We use 4 isofemale lines of the mosquito and let the parasites infect 4 replicates of various combinations of these lines over several generations : (i) a single line, (ii) a mixture of the 4 lines, and (iii) a switch of the line each (host) generation. Through this experimental design, we will be able to follow the process of specialization on each line and generalization on the mixtures of lines. Considering the efficacies (and within-host growth) of each strain of parasites on each of the isofemale lines will give an indication of the trade-offs involved in specialization and thus improve our understanding of specialist and generalist parasites.

10.19P

ADAPTIVE RADIATION AND THE FATE OF MUTATOR BACTERIA

[1]R. C. MacLean, [2]P. B. Rainey, [1]G. Bell

[1]*McGill University, 1205 Ave. Dr. Penfield, Montreal H3A 1B1, Canada*

[2]*University of Oxford, South Street, Oxford OX1 3R8, UK*

Mutator alleles can hitch-hike to high frequency in non-recombining bacterial populations that are adapting to a novel environment because of linkage between mutator alleles and the beneficial mutations they create. The goal of our experiment was to test the hypothesis that hitch-hiking should be more likely during bouts of adaptive radiation, when selection is diversifying, than adaptation, when selection is directional. To test this hypothesis we introduced an isogenic mutator strain into a clonal population of the bacterium *Pseudomonas fluorescens* that was allowed to adapt to novel homogeneous and heterogeneous microcosms. Selection was primarily directional in homogeneous microcosms, and diversity did not evolve. Diversifying selection in heterogeneous environments lead to the rapid evolution of ecological and genetic diversity. Mutators were much more successful at invading heterogeneous environments than homogeneous environments. In heterogeneous microcosms, the frequency of the mutator was well correlated with the frequency of novel niche-specialist morphotypes, demonstrating that diversifying selection, and not environmental heterogeneity *per se*, facilitated the invasion of the mutator strain in heterogeneous microcosms. These results clearly demonstrate that the likelihood of mutators hitch-hiking to high frequency is greatest when ecological conditions generate diversifying selection.

10.20P

CHANGE IN FITNESS IN *CHLAMYDOMONAS REINHARDTII* IN LONG TERM SEXUAL VERSUS ASEXUAL SELECTION LINES

[1]Sebastien Renaut, [2]Graham Bell

[1]*McGill University, Stewart Biology Building, 1205 Dr Penfield Avenue, Montreal, Canada H3A 1B1*

[2]*McGill University, Redpath Museum, 859 Sherbrooke Street West, Montreal, Canada H3A 2K6*

We performed a long term selection experiment with the unicellular chlorophyte *Chlamydomonas reinhardtii* to investigate the fitness effects of sexual and asexual reproduction. Sexual reproduction is expected to get rid of mildly deleterious mutations faster (mutation clearance) and thus increase the overall fitness of a sexual population compared to an asexual one. In the past, fitness has been assayed using many different experimental procedures in *Chlamydomonas*. In order to have a good general idea of the effect of mutation clearance in our selection lines, we used different methods looking at the competitive nature of fitness or at the growth rate of a population in pure culture. We can then compare and contrast the fitness values obtained with the different methods. The results seem to show only a small advantage of sexual reproduction. Different values were also obtained depending on the method which leads to a more ambiguous interpretation of the data.

10.21P

THE INVASION OF MUTATOR CELLS IN EXPERIMENTAL POPULATIONS OF *E. COLI*

D. E. Rozen, J. A. G. M. de Visser

Laboratory of Genetics, Wageningen University, Wageningen 6703 BD, The Netherlands

The evolution of mutation rates has been a consuming problem for evolutionary biologists for half a century. While new mutations are essential for adaptation, most mutations are harmful; thus, increased mutation rates are likely to be generally disadvantageous. These competing factors have led to the compromise position that population wide mutation rates will tend to evolve towards the minimal rate required for adaptation but no higher, thus preventing an ever accumulating load of deleterious mutations. The reality, however, is complicated by the fact that natural sub-populations of bacteria are often found with vastly increased mutation rates. Here we examine factors contributing to the successful invasion of such anomalous mutators.

Chao and Cox (1983) classically demonstrated that mutator clones of *E. coli* invade wild-type populations in a frequency-dependent manner: at frequencies equal to or greater than the product of their relative population size and mutation rate, mutators invaded because they were the first subpopulation to produce a beneficial mutation. Below this equivalency point the wild-type cells won. Closer examination of the classical data, plus new data presented here, show that, in fact, mutator subpopulations invade at initial frequencies significantly lower than the predicted equivalency cut-off. Two hypotheses might account for this discrepancy: 1) actual beneficial mutation rates of mutators are vastly underestimated by fluctuation tests; or 2) mutator cells produce a distribution of beneficial mutations that is different from that produced by wild-type cells, with a bias towards mutations that confer larger benefits. Here we provide support for this latter hypothesis, which indicates an additional and heretofore unconsidered advantage to mutator cells. Explanations and implications for these results are discussed.

10.22P

CHARACTERIZATION OF THE DISTRIBUTION OF MUTATIONAL EFFECTS FOR AN RNA VIRUS

R. Sanjuán, A. Moya, S. F. Elena

Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Universitat de València, P.O. Box 22085, 46071 València, Spain

Instituto de Biología Molecular y Celular de Plantas, CSIC, Avenida de los naranjos s/n, 46022 València, Spain

RNA viruses are characterized by mutation rates well above 1 per genome and replication round. This characteristic, together with huge population sizes and fast generation times are the reason for the enormous adaptive potential shown by RNA viruses. Despite its importance, very little is known about the distribution of mutational effects caused by point mutation in RNA viruses. Similarly, almost nothing is known about how multiple mutations interact in determining viral fitness. Here, we took an experimental approach to analyze these two important issues. In a first step, we generated a collection of 92 single-site mutants of vesicular stomatitis virus (VSV) by site-directed mutagenesis on an infectious cDNA. Half clones recreated substitutions already found in natural or laboratory populations, whereas the other half were chosen randomly. These clones were transfected into BHK-21 cells and fitness was determined for each of them, as well as for their non-mutated ancestor. In a second step, we plan to generate a collection of double mutants. From this distribution, we will infer the abundance and predominant direction of epistasis in an RNA genome.

10.23P

ADAPTIVE LOSS OF GENES AND FUNCTIONAL ANALYSIS OF THE YEAST GENOME

Piotr Sliwa, Korona Ryszard

Institute of Environmental Sciences, Jagiellonian University, 30-387 Krakow, Poland

Numerous genes, either with known or unknown function, can be knock-out and the organism is seemingly not affected. It is possible that some genes are indeed unnecessary, or perhaps maladaptive in some environments, but are maintained by natural selection because their net effect over all possible environments is positive. Two straightforward research questions emerge: How often deletion of a gene is adaptive in at least one environment? What are consequences of such "adaptations" in other environments? The present study employs a commercially available collection of individually recognisable single-gene deletions covering the whole yeast genome. These deletion clones was competed against an isogenic wild-type strain in serial transfer cultures. Clones suspected for carrying an adaptive deletion were identified at the molecular level, i.e. their deleted loci found. Results of the so far completed assays suggest that as much as about 1-2% of deletions can be actually slightly adaptive under standard laboratory conditions. The whole selection procedure was done in an "optimal" environment. However, once adaptive deletions are identified, their pleiotropic effects can be found by testing for growth on a wide spectrum of specific yeast media designed to uncover defects in different cellular functions and structures.

10.24P

HORIZONTAL ACQUISITION OF DIVERGENT CHROMOSOMAL DNA: THE EFFECTS OF MUTATOR PHENOTYPES

[1]Jeffrey P. Townsend, [2]Kaare M. Nielsen, [3]Daniel S. Fisher, [4]Daniel L. Hartl

[1]*University of California, 111 Koshland Hall, Berkeley, CA 94720*

[2]*University of Tromso, N-9037 Tromso, Norway*

[3]*Harvard University, 17 Oxford Street, Cambridge, MA 02138*

[4]*Harvard University, 16 Divinity Avenue, Cambridge, MA 02138*

We examine the potential beneficial effects of the expanded access to environmental DNA offered by mutators on the adaptive potential of bacterial populations of *E. coli*. Using parameters from published studies of recombination in *E. coli*, we find that the presence of mutators has the potential to greatly enhance bacterial population adaptation when compared to populations without mutators. In one specific example, for which 3 specific amino acid substitutions are required for adaptation to occur in a 300 amino acid protein, we found a 3500-fold increase in the rate of adaptation. The probability of a beneficial acquisition decreased if more amino acids changes, or integration of longer DNA fragments, were required for adaptation. The model also predicts that mutators are more likely to acquire genetic variability from a more diverged set of donor bacteria than nonmutator phenotypes. Bacterial populations harboring mutators in a sequence heterogeneous environment are predicted to acquire most of their DNA conferring adaptation in the range of 13-30% divergence, whereas nonmutator phenotypes become adapted after recombining with more homogeneous sequences of 7-21% divergence. We conclude that mutators can accelerate bacterial adaptation when desired genetic variability is present within DNA fragments of up to ~30% divergence.

10.25P

FEATURES OF ADAPTATION IN CONTINUOUS YEAST CULTURES (*SACCHAROMYCES CEREVISIAE*)

David E. Wembridge, Austin Burt

Imperial College London, Silwood Park Campus, Ascot, Berkshire, SL5 7PY, UK

Abstract not available

10.26P

SMALL FITNESS EFFECTS AND WEAK GENETICS INTERACTIONS BETWEEN DELETERIOUS MUTATIONS IN HETEROZYGOUS LOCI OF THE YEAST *SACCHAROMYCES CEREVISIAE*

[1]Dominika M. Wloch, [1]Krzysztof Szafraniec, [1]Piotr Sliwa, [2]Rhona H. Borts, [1]Ryszard Korona

[1]*Jagiellonian University, Institute of Environmental Sciences, ul. Gronostajowa 3, 30-387 Krakow*

[2]*University of Leicester, Genetics Department, LE1 7RH, Great Britain*

Random and relatively infrequent mutations were induced in budding yeast by ethylomethan sulfonate (EMS). Clones known to bear non-neutral mutations were used to obtain mutant heterozygotes and mutant homozygotes that were later compared with the wild-type homozygotes. An average homozygous effect of mutation was about 2% decrease in the growth rate. In heterozygotes, the harmful effect of these relatively mild mutations was reduced by about four times. In a test of epistasis, two heterozygous mutant loci were paired at random. Fitness of the double mutant was best explained by multiplicity of single-locus effects, leaving little space for epistatis and practically excluding synergistic interaction. In other experiments, the same mutations in haploid and heterozygous diploid clones were compared. Regardless what were the haploid phenotypes, mildly deleterious or lethal, fitness of the heterozygotes was decreased by less than half percent on average. It implies that our recent estimates of mutation rate were based on the correct assumption that mutations were not selected out of populations when masked by the wild type alleles. More generally, the present results suggest that heterosity makes the genetic basis of the quantitative traits smooth and flat, which is, most mutations tend to exhibit small and poorly interacting effects.

Symposium 11

Pollinators and plant evolution - from specialists to generalists

Organisers: Christine B. Mueller & James M. Cook

Conference Auditorium 1

09.20 – 09.50	**Ollerton, J.** Patterns of specialization and generalization in pollination systems across ecosystems
09.50 – 10.20	**Smithson, A.** Cheating plants, pollinator learning, and specialisation by plants and pollinators
10.20 – 11.00	**Coffee**
11.00 – 11.20	**Castellanos, M. C.** Pollen transfer and evolutionary shifts to hummingbird pollination in *Penstemon*
11.20 – 11.40	**Collin C. L.** Should *Dianthus sylvestris* cater to a specialist pollinators that eats its seeds?
11.40 – 12. 00	**Cook, J. M.** Impacts of pollinating fig wasps on the evolution of their host plants
12.00 – 12.20	**Memmot, J.** Generalization in pollination systems: a food web approach
12.20 – 12.40	**Schiestl, F. P.** Insect behavior and floral evolution in sexually deceptive orchids
12.40 – 14.00	**Lunch**

Invited talks

11.1

PATTERNS OF SPECIALIZATION AND GENERALIZATION IN POLLINATION SYSTEMS ACROSS ECOSYSTEMS.

[1]**Jeff Ollerton**, [2]Steve Johnson, [3]Andrew Hingston

[1]*University College Northampton, Park Campus, Northampton, NN2 7AL, UK*

[2]*University of Natal, Pietermaritzberg, South Africa*

[3]*University of Tasmania, Hobart, Australia*

Biologists have been describing and cataloguing plant-pollinator interactions for almost two hundred years and there now exists an enormous, if diffuse, data set. Perhaps because the data are so scattered, there has been only a limited attempt at synthesising and comparing these data to investigate the broad details of the biogeography of specialization, generalization, and relative commonness of pollination systems. Such studies that do exist concentrate either on specific plant families, or form part of larger, more general reviews. We are largely ignorant of the answers to questions such as: are plant-pollinator interactions more specialized in the tropics? Are there differences between the Old World and the New World in the relative commonness of particular pollination systems? How does phylogeography influence such patterns that do exist? Using a database of published and unpublished community-level surveys of plant-pollinator relationships, we have conducted a series of analyses which provide a first approximation to these questions and, we hope, will open up this debate. Our results suggest that tropical plant-pollinator interactions are not, on average, more ecologically specialized. In addition, we categorised pollination systems broadly (wasp, hawkmoth, large bee, etc.) and looked at the importance of latitude, longitude, altitude, biome type and phylogeny on the particular mix of pollination systems found within a community. Comparative multivariate analysis of the proportions of different pollination systems across the biosphere suggest that there is a strong biogeographical structure to the relative importance of different pollination systems and we discuss reasons why this may be the case.

11.2

CHEATING PLANTS, POLLINATOR LEARNING, AND SPECIALISATION BY PLANTS AND POLLINATORS

A. Smithson

University of Exeter, School of Biological Sciences, Hatherly Labs, Prince of Wales Road, Exeter EX4 4PS, UK

The ancestral angiosperm species has been suggested to have a very simple flower structure: bowl-shaped, with pollen used as an insect reward. Today, many angiosperm species have evolved far more complex adaptations for pollination. One example are long spurs which hold reservoirs of nectar for pollinators: the most extreme examples can be found in the genus *Agraecum* (Orchidaceae). The evolution of such complex floral morphology has been seen as a way of restricting access to the nectar to specific pollinators, which are the most abundant or effective at transferring pollen, thus resulting in specialisation. Alternatively, Bell predicted that plants whose nectar is more deeply concealed within a flower would be able to produce a larger proportion of flowers without nectar: thus the evolution of complex morphology such as nectar-hiding spurs allows the plant to be able to 'cheat'. From a pollinators' perspective generalisation permits the utilisation of more food resources, and is costly in terms of the greater behavioural flexibility required, but does potentially allow the pollinator to learn and avoid plants that 'cheat'. In this talk I will examine whether plants have evolved floral complexity through pollinator specialisation or through the advantage of nectar concealment. I will also explore whether pollinator generalisation allows learned avoidance of cheating plants.

Contributed talks

11.3

POLLEN TRANSFER AND EVOLUTIONARY SHIFTS TO HUMMINGBIRD POLLINATION IN *PENSTEMON*

[1]**M. C. Castellanos,** [2]P. Wilson, [1]J. D. Thomson

[1]*Department of Zoology, University of Toronto, 25 Harbord St., Toronto, ON M5S 3G5, Canada*

[2]*Department of Biology, California State University, Northridge, CA 91330-8303, USA*

From the plant's perspective, pollinators differ in their abilities to transfer pollen. Variation in pollination efficiency could help explain evolutionary shifts between types of pollination in some plant groups. Flowers of species in the genus *Penstemon* (Scrophulariaceae) can be arrayed along a "syndrome gradient" from having characters associated with bee- and wasp- pollination to having characters associated with hummingbird-pollination. A phylogeny of the group shows that evolution along this gradient (pollinator shifts) has occurred at least 13 times. We hypothesized that differences in pollen transfer by hummingbirds and bees might account for the repeated transitions to hummingbird pollination. We tested this by comparing the two pollinators visiting bee-adapted *Penstemon strictus* and bird-adapted *P. barbatus*. We also experimentally modified flowers to study whether specific floral characters predominantly change to exclude less efficient pollinators (bees in this case) or/and to improve the morphological fit between flowers and hummingbirds. Our results indicate that if birds were to visit bee-adapted penstemons frequently enough, they would immediately be as good pollinators as bees. We propose that a change in nectar rewards that makes a *Penstemon* patch more attractive to hummingbirds can trigger further adaptation to hummingbird pollination by simple floral changes. In some cases, such changes include characters that explicitly exclude bees. Shifts towards more specialized hummingbird pollination can be explained under such conditions, but interestingly, there are still more bee-adapted penstemons than bird-adapted penstemons.

11.4

SHOULD *DIANTHUS SYLVESTRIS* CATER TO A SPECIALIST POLLINATORS THAT EATS ITS SEEDS?

Carine L. Collin, Jacqui A. Shykoff

Université Paris-Sud, Bât. 360, F-91405 Orsay cedex, France

The rock pink *Dianthus sylvestris* (Caryophyllaceae) is a gynomonoecious - gynodioecious species that presents a sexual dimorphism in flower size. Small pistillate and large perfect flowers can be found on different plants (females and hermaphroditic, respectively) or together on mixed plants. It is visited by several Lepidoptera as well as by some Syrphid flies, but only the diurnal European hawk-moth *Macroglossum stellatarum* (Sphingidae) and the nocturnal moth *Hadena compta* (Noctuidae) are known to be efficient pollinators. *M. stellatarum* is a generalist pollinator that feeds on nectar from many other species whereas *H. compta* is rather specialised on *D. sylvestris*. Indeed females *Hadena* use the flowers as oviposition sites, the young caterpillar feeding on ovules and developing seeds. The relationship between *Dianthus* and *Hadena* is more likely to be parasitism than mutualism. A single caterpillar feeds on several capsules until pupation. Therefore the progeny of a pair of *Hadena* moths certainly provoke more damage to plants than the adults give pollination. Through results of several experiments (pollinator exclusion, pollen limitation, fluo dye dispersion...) we investigated the pollination of pistillate and perfect flowers of *D. sylvestris* by both *Hadena* and *Macroglossum*. We discuss whether this species should specialise on pollination by *Hadena* despite strong predation or promote pollination by generalists. Further we discuss the influence of this pollinating system on the evolution of the sexual dimorphism often found in gynodioecious species.

11.5

IMPACTS OF POLLINATING FIG WASPS ON THE EVOLUTION OF THEIR HOST PLANTS

James M. Cook

Imperial College London, Silwood Park Campus, Ascot, Berks SL5 7PY, UK

The major processes of evolution are adaptation and speciation and closely interacting species, such as plants and specialist pollinators, may influence each other's adaptation, speciation, both or neither. We are investigating these issues using the model system of figs (*Ficus*) and their fig-pollinating wasps (family Agaonidae), of which there are around 750 pairs of species. In terms of adaptation, comparative studies at both high and low taxonomic levels show a very strong correlation between pollination behaviour and pollen investment (floral sex ratios). Figs with active pollinators produce much less pollen than those with passive pollinators and there have been several phylogenetically independent changes that support the correlation. In terms of speciation, less is known, but it is clear that the phylogenies of figs and fig wasps show significant congruence. However, we ask whether wasps drive fig speciation, figs drive wasp speciation, or speciation is relatively independent in the two groups. As long as host shifts are rare, many speciation scenarios are consistent with parallel phylogenesis.

11.6

GENERALIZATION IN POLLINATION SYSTEMS: A FOOD WEB APPROACH

Jane Memmott

School of Biological Sciences, University of Bristol, Woodland Road, Bristol, BS8 1UG

Most interactions between plants and their pollinators are embedded in a complex web of plant-pollinator interactions. These plant-pollinator webs can be studied in the manner of conventional food webs and the aim of this talk is to illustrate how contemporary methods of web construction and analysis can be applied to plant-pollinator communities.

11.7

INSECT BEHAVIOR AND FLORAL EVOLUTION IN SEXUALLY DECEPTIVE ORCHIDS

Florian P. Schiestl

Geobotanical Institute ETH, Zollikerstrasse 107, CH-8008 Zürich, Switzerland

Sexually deceptive orchids mimic sex pheromones and appearance of female insects and thus attract only male pollinators which pollinate the flowers in an attempted mating. Male mating behavior is crucial for pollination and pollinator attraction is highly specific, therefore, the behavior of the pollinators is likely to impose selection pressures on the evolution of flowers. In this first experimental approach with controlled olfactory and visual stimuli I investigate male mate-choice behavior in the pollinator of a sexually deceptive orchid and its consequences for the evolution of floral traits in the orchid. My study system is the Australian Thynnine wasp *Neozeleboria cryptoides* (Smith)(Hymenoptera: Tiphiidae), which pollinates the orchid *Chiloglottis trapeziformis* Fitzg.. 1) When males of the pollinator were given the choice between two dummies of different sizes (with identical amount of synthetic pheromone), they preferentially attempted to copulate with middle size dummies (approximately the size of a flower labellum) over small size dummies (size of a female). They did, however, not prefer large dummies (size exceeding a flower) over small dummies. 2) When given the choice between two dummies of identical size with different amounts of pheromone, males always preferred the larger amount of pheromone, except if very small amounts were used. Larger amounts of pheromone generally attracted more males than smaller amounts. 3) When five dummies were offered simultaneously in a 10 cm circular array, males rarely attempted copulation on more than one dummy during one visit. 4) Orchid flower labella, the mimic of a female body, were significantly longer and broader than female bodies. Flowers also produced on average ten times more "pheromone" than females. Under pollination limitation, the evolution and maintenance of these exaggerated mating signals is likely to be mediated by the here demonstrated male pollinator behavior.

Posters

11.8P

BUTTERFLY PROBOSCIS LENGTH AND FLOWER DEPTH: AN EXPERIMENTAL STUDY ON POLLEN DEPOSITION

Daniel Bloch, Andreas Erhardt

University of Basel, St.-Johanns-Vorstadt 10, 4056 Basel, Switzerland

Coevolution of plants and pollinating insects is a long standing paradigm for evolutionary processes. Pollinator mediated selection on floral traits has repeatedly been documented. However, selective effects of different pollinators on intraspecific phenotypic variation of floral traits has been studied less frequently. Here we report findings on pollen deposition of two different butterfly species (*Melanargia galathea* and *Inachis io*), differing in proboscis length (12.7 ± 0.7 mm (SD), 15.1 ± 0.4 mm (SD), respectively), on flowers of the butterfly pollinated plant species *Dianthus carthusianorum*, varying in floral depth (calyx length, length of stamens, stigma height). Using an experimental approach allowed to separate effects of male and female floral components as well as effects of tongue length of the two pollinators on pollen deposition. Results indicate that (1) pollen deposition differed in quantity but not in quality between the two butterfly species; *I. io* deposited significantly more pollen than *M. galathea.* (2) The number of pollen grains deposited on stigmas was negatively correlated with both, stamen length and stigma height. (3) Although correlated with the length of reproductive floral parts, calyx length itself was not anymore significantly correlated with pollen transfer. These results suggest not only directive selection for a reduction of flower depth under a pollinator regime dominated by butterflies with similar tongue lengths as in the two tested species, but shows also that proboscis length is a critical factor for pollen deposition in this butterfly pollinated plant species.

11.9P

VICTIMS OF THEIR SENSORY BIASES: RECEIVER PSYCHOLOGY OF HONEYBEES (*APIS MELLIFERA*) EXPLOITED BY CRAB SPIDERS (*THOMISUS SPECTABILIS*)

Astrid Heiling

Inst. Zoology, Univ. Vienna, Alhanstrasse 14, A-1090 Vienna Austria

Flower signals exploit the pre-existing sensory biases of their receivers and modulate their behaviour. In the communication system between plants and pollinating insects, both parts profit, either through reproductive service, or through gaining nectar- or pollen-rewards. However, intruders can benefit if they have the sensory capabilities to perceive and process information that match the sensory biases of intended receivers. This is obviously the case for *Thomisus spectabilis* (Thomisidae). These crab spiders sit on flowers where they ambush pollinating insects such as honeybees. Their body colour ranges from white (UV-reflecting) to yellow (UV-absorbing) and the colouration either matches the flower background or contrasts against it. Choice experiments revealed that crab spiders creating an UV-reflecting mark against the flower background attract honeybees (*Apis mellifera*) to the flower, while UV-absorbing marks are avoided. Only if there is no colour contrast between crab spider and flower, the signalling system between plant and pollinator is not effected by the predator. Field observations showed that *T. spectabilis* are not randomly distributed between flowers of different colours. Lab experiments confirmed that these spiders are able to perceive visual flower signals and go for colours, which, according to their own colouration, are most beneficial in terms of prey capture. *T. spectabilis* are able to exploit flower signals and even to manipulate them by creating unhonest signals. Our results highlight the importance of considering both sensory physiology and actual signal response by a receiver in studies of signalling systems.

11.10P

POLLINATORS AND THE EVOLUTION OF THE WILD PLANT *ECHIUM VULGARE*

Kirsten A. Leiss, Peter G. L. Klinkhamer

Institute of Biology, Leiden University, Kaiserstraat 63, 2311 GP Leiden, Netherlands

In a natural population of *Echium vulgare* a wide range of nectar was produced. Nectar production was strongly hierarchic with a few high nectar producing plants dominating the population (Gini coefficient = 0.86, 95% CI interval = 0.81 - 0.89) and had a clumped spatial distribution (Moran's I = 0.17, P = 0.001). High nectar production increased the number of pollinator visits (r = 0.353, P = 0.005) and boutlength (r = 0.261, P = 0.042). Results suggest the opportunity for selection of high nectar production. In contrast, heritability of nectar production was relatively low both, under controlled ($h^2 = 0.13$) and field ($h^2 = 0.26$) conditions. While there was no difference in nectar production of offspring of high nectar producing plants between the two environments (P = 0.785), nectar production of the offspring of low producing plants was significantly larger under controlled conditions compared to the field (P = 0.009) indicating a genotype by environment interaction. Based on these results we may expect a correlation to have evolved between nectar production rate and level of inbreeding. If high nectar production increases boutlength it may increase inbreeding, which would be an advantage in adaptation to a stable environment favourable to nectar production.

11.11P

SEXUAL DECEPTION IN ORCHID POLLINATION

Jim Mant

Geobotanical Institute, ETH Zurich, Zollikerstrasse 107CH-8008 Zurich, Switzerland

Orchids of the genus *Chiloglottis* are pollinated through the sexual deception of male wasps mainly from the genus *Neozeleboria* (Tiphiidae: Thynninae). The orchids mimic both the appearance and sex pheromones of wingless female thynnines but provide no reward to the deceived males. Despite the asymmetry of this interaction, strong pollinator specificity is typical. Such plants might be expected to be relatively flexible in their adaptive response to variation in the local pollinator resource. However, DNA sequence data is presented on both orchids and wasps that demonstrate a pattern of pollinator conservatism operating at a range of taxonomic levels. Sequence data from the wasps indicate 15 of 16 *Chiloglottis* pollinators are closely related members of one clade of Thynninae. A pattern of congruence between orchid and wasp phylogenies is also demonstrated below the generic level, such that related orchids tend to use related thynnine wasps as specific pollinators. Comparative physiological data on the wasp responses to the floral scents of two *Chiloglottis* species and one outgroup, *Arthrochilus*, indicate similar attractive volatile chemicals are used by related orchid taxa. By extension, a similarity of sex pheromone signals among related thynnines is inferred. Thus, the conservative pattern of pollinator change in sexually deceptive orchids may reflect phylogenetic patterns in the sex pheromones of their pollinators.

11.12P

DISPERSAL BY GEMMAE AND SPORES IN BRYOPHYTES

[1]M. Pohjamo, [2]S. Laaka-Lindberg, [1]H. Korpelainen

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

[2]University of Helsinki, Lammi Biological Station, 16900 Lammi, Finland

Dispersal ability is of great importance for bryophytes, which commonly occupy spatially limited habitat patches. Bryophyte dispersal has been thought to take place primarily by spores. However, another potential mechanism is dispersal by diaspores, such as gemmae and leaf fragments, which are not produced by meiosis. In this presentation, we report results concerning the dispersal range of the boreal leafy hepatic *Anastrophyllum hellerianum*, which was studied in an old-growth forest in Southern Finland. *A. hellerianum* is a dioicous species which reproduces both sexually by spores and asexually by one-celled gemmae. Dispersal ability is essential for species inhabiting temporal, patchily distributed substrate such as decaying wood, on which *A. hellerianum* is specialized to grow. As the production of spores is rare (only in 12.5 % of the colonies in the study area), the ability of *A. hellerianum* to colonize new substrate patches by asexual gemmae is crucial. The dispersal of gemmae was studied by traps made of vaseline-covered microscope slides distributed in each of eight compass directions at distances of 0-10 m from the parent colony. This experiment was conducted both in a natural habitat and in an artificial set-up without background dispersal. To study the role of animals in dispersing gemmae, the potential gemma-vectors, ants (*Sanguinea rufa*) were allowed to move over a mat of gemmiferous shoots of *A. hellerianum*, and then across vaseline-covered traps located at regular intervals of 0.1-30 m from the gemma-mat. The results indicate that asexual gemmae may function in dispersal over relatively long distances, which is comparable to the dispersal of spores on a local scale, and that animal-vectors have a role in bryophyte dispersal. Additionally, we are in the process of tracking the dispersal routes of bryophytes along a network of ant paths using genetic markers.

Symposium 12

Evolution of sexual communication in insects

Organisers: Astrid Groot & Anneli Hoikkala

Conference Auditorium 2

09.20 – 09.50	**Löfstedt, C.** A phylogenetic reconstruction of the evolution of moth pheromone communication
09.50 – 10.20	**Ritchie, M. G.** Title unavailable
10.20 – 11.00	**Coffee**
11.00 – 11.20	**Cremer, S.** Being attractive to both sexes: chemical female mimicry of ant males
11.20 – 11.40	**LeBas, N. R.** Non-linear and correlational sexual selection on ‘honest’ female ornamentation
11.40 – 12. 00	**Jones, T. M.** The importance of being average
12.00 – 12.20	**Groot, A.** Evolution of moth pheromone communication systems
12.20 – 12.40	**Serrano-Meneses, A.** Disentangling the mechanisms of selection for male wing pigmentation in calopterygid damselflies: sexual or natural selection?
12.40 – 14.00	**Lunch**

Invited talks

12.1

A PHYLOGENETIC RECONSTRUCTION OF THE EVOLUTION OF MOTH PHEROMONE COMMUNICATION

Christer Löfstedt

Department of Ecology, Lund university, Ecology building, SE-223 62 Lund, Sweden

Olefinic fatty acid derivatives (including acetates, alcohols and aldehydes with one or more double bonds and 10-18 carbon atoms) are used as pheromone components throughout the Lepidoptera, whereas the use of polyenic hydrocarbon pheromones is mainly restricted to the superfamilies Noctuoidea and Geometroidea. The two pheromone types differ in their biosynthesis and are derived from distinctly different precursors. Olefinic acetates are biosynthesized from palmitic acid (and shorter or longer homologues) by interaction with different acyl-CoA desaturases, in contrast to the polyenic hydrocarbons that may be derived from linoleic or linolenic acid by decarboxylation. Primitive moths use a third type of pheromone components, i.e. short-chain alcohols and ketones, which have previously been assigned a defensive function in Trichoptera, the sister group of Lepidoptera. A phylogenetic reconstruction of pheromone evolution in the Lepidoptera reveals that short-chain alcohols evolved into species-specific mate recognition signals in the early evolution of Lepidoptera. Cryptic species making use of specific ratios of (*R/S*)-(*Z*)-6-nonen-2-ol were demonstrated among leaf-miners of the genus *Eriocrania* by means of RAPD-analysis. The most common type of moth pheromone consisting of long-chain olefinic acetates, aldehydes or alcohols, evolved in the divergence of the heteroneuran lineages, prior to the evolution of ditrysian moths. The evolution of this type of pheromone may have given rise to adaptive radiation, potentially being an explanation for the large number of species among ditrysian moths. Polyenic hydrocarbons emerged more recently in moth evolution. A phylogenetic analysis of pheromone diversity among geometroid moths reveals that the genes involved in the biosynthesis of hydrocarbon pheromones may have been switched on and off on several occasions. The switch between two types of pheromone systems is intriguing as it involves the coevolution of a different biosynthetic machinery and pheromone component receptors with different characteristics. These are major evolutionary changes compared to a change in ratios between pheromone components, which is frequently observed among closely related species. Evolutionary and molecular mechanisms involved in the gain and loss of pheromone components in the evolution of moth pheromone communication will be discussed, including additional examples from primitive moths, noctuids, pyralids and yponomeutids.

12.2

TITLE NOT AVAILABLE

Michael G. Ritchie

University of St Andrews, Dyers Brae, St Andrews, UK

No abstract available but no doubt it will be an excellent talk, as usual!

Contributed talks

12.3

BEING ATTRACTIVE TO BOTH SEXES: CHEMICAL FEMALE MIMICRY OF ANT MALES

[1]**Sylvia Cremer**, [2]Matthew F Sledge, [3]Juergen Heinze

[1]*Zoological Institute, Department of Population Ecology, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen, Denmark*

[2]*Department of Animal Biology and Genetics, Università degli Studi, Via Romana 17, 50125 Florence, Italy*

[3]*Biology 1, University of Regensburg, Universitaetsstr. 31, 93040 Regensburg, Germany*

In the ant *Cardiocondyla obscurior*, two discrete male morphs compete for the access to female mating partners. Wingless males have evolved escalated fighting to monopolize matings with the young emerging queens in the nest. Winged males, by contrast, are specialized for mating in a swarm flight, and do not fight at all. Interestingly, winged males also mate inside the nest before emigration, thus representing a major threat for the reproductive success of the exclusively locally mating wingless males. Winged males should thus be attacked by the wingless fighter males when trying to mate in the nest. We found that winged males circumvent this threat by using a tactic of deception in sexual communication: they perform a female mimicry by expressing a female-like chemical profile ("odour") on their cuticle, which does not only prevent them from attacks, but even renders them attractive mating partners for the wingless males. Despite all other differences between the two male morphs, their mating behaviour is the same succession of stereotypic antennation and mounting movements, and both male types gather equal mating success with the queens. The observed chemical deception seems to be the underlying mechanism allowing the coexistence of the two alternative reproductive tactics in males of the ant *Cardiocondyla*. However, the swindle is likely costly for winged males and is only expressed when they are too young and immature for flying out. After loosing their protective chemical signature, winged males show a change in behavior and seem to avoid contact with the aggressive males. Interestingly, female mates and the winged males themselves do not seem to be fooled by their chemical similarity, thus likely using different path of sexual communication that is less susceptible for deception.

12.4

NON-LINEAR AND CORRELATIONAL SEXUAL SELECTION ON 'HONEST' FEMALE ORNAMENTATION

N. R. LeBas, L. R. Hockham, M. G. Ritchie

University of St Andrews, Dyers Brae, St Andrews, UK

Females are not expected to invest in ornamentation unless the fitness benefits of the ornament exceed those derived from investing the resources directly into offspring. Hence the circumstances under which females would benefit from investing in sexually selected traits are limited. However, in the empidid dance flies, it is usually the female, rather than the male, which is ornamented. Dance fly males provide females with nuptial gifts and in many species females have lost the ability to hunt. Ornamental female traits in empidids such as abdominal sacs and enlarged pinnate leg scales, have been proposed to 'deceive' males into matings by exaggerating female abdomen size. In the dance fly, *Rhamphomyia tarsata*, males provide nutritious nuptial gifts and females are ornamented with enlarged pinnate leg scales. We quantified selection in the field on *R. tarsata* and found escalating, quadratic sexual selection on female pinnate scales. We also show that pinnate scales are actually an honest indicator of female fecundity. Selected females had a larger number and more mature eggs than unselected females, highlighting the benefit rather than cost of male choice. We also show correlational sexual selection on ornamentation and fecundity, which may ensure honesty in female ornamentation.

12.5

THE IMPORTANCE OF BEING AVERAGE

T. M. Jones, M. A. Elgar

Department of Zoology, The University of Melbourne, 3010 Victoria, Australia

Models of age-related mate choice predict female preference for older males as they have proven survival. However, these models rarely address differences in male mating history when evaluating the potential benefits gained by females from older partners. Moreover, few studies consider the role of cues used in mate choice despite the potential for age-related degradation. We used a novel experimental design to assess simultaneously the relative importance of these parameters in the hide beetle, *Dermestes maculatus*. Male hide beetles possess a gland on their ventral surface that emits pheromones used in aggregation and mate selection. We present a two part experiment that first explores age-related female preferences and then examines the consequences of such preferences while controlling for male age and mating history. When presented with a choice of males varying in age, females preferentially mated with intermediate-age males. To test the consequences of such age-related mating preferences, a second set of females were mated to males varying in age (young, intermediate-age and old) and mating history (numbers of previous matings). Comparison across these females showed that male age was a critical determinant of reproductive success. Females mated to intermediate-aged males enjoyed consistently higher fecundity and fertilisation. In contrast, the oldest males spent longer courting females, but were less fertile. A male's previous mating history determined his current reproductive effort; virgin males spent longer in copula than males with prior mating opportunities. However, this did not translate into differences in fertilisation success. We propose that age-related female preference in the hide beetle is based on chemical cues which potentially degrade with male age. Our experiments further indicate that preference for intermediate-aged males is maintained in this species through fertilisation benefits accrued by discriminating females.

12.6

EVOLUTION OF MOTH PHEROMONE COMMUNICATION SYSTEMS

Astrid Groot, Fred Gould, Coby Schal

Department of Entomology, North Carolina State University, Raleigh, NC 27695-7634, USA

Most night-flying moth species locate mates through production of, and response to, a very precise blend of three or more volatile chemical compounds. The genes that control pheromone blend ratios have never been found to be linked to, or affect male response, so mutations that cause changes in each of the two components of communication are expected to arise independently. Within a population, females with atypical blends have been shown to be less attractive to males than females with the population's common blend. Similarly, rare males that respond to atypical blends are expected to be at a disadvantage in finding mates. On a simple theoretical level, this type of sexual communication system is expected to be evolutionarily constrained or static because an individual with a mutation leading to an altered blend or response will be selected against, when rare. Even if the selective disadvantage to rare individuals with alleles for novel signals or responses is minimal, mass selection is not expected to increase their frequency in the population. At least two hypotheses could explain the evolution of diverse patterns of chemical communication among moth species. First, existing studies showing mating disadvantage only examined a limited set of traits, and did not search for environmental conditions in which the selective disadvantage was negated, so results may not be representative. Second, it is possible that the population structure of moths enables the evolution of new sexual communication systems through a combination of genetic drift and selection. We are addressing these hypotheses by identifying Quantitative Trait Loci (QTL) that alter sexual communication traits, and their impacts on mating fitness. Our studies are conducted with two closely related moth species, *Heliothis virescens* and *H. subflexa.*

12.7

DISENTANGLING THE MECHANISMS OF SELECTION FOR MALE WING PIGMENTATION IN CALOPTERYGID DAMSELFLIES: SEXUAL OR NATURAL SELECTION?

[1]**Alejandro Serrano-Meneses**, [2]Alejandro Córdoba-Aguilar

[1]*Department of Biology and Biochemistry, University of Bath, 4 South, Claverton Down, Bath, BA2 7AY, UK*

[2]*Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo, Apdo. Postal 69-1, Plaza Juárez 42001, Pachuca, Hidalgo, Mexico*

Male wing pigmentation is a fascinating and unique characteristic of several dragonfly families including the Calopterygidae. Two hypotheses explain the evolution and maintenance of this trait: a) Mate recognition: wing pigmentation aids females to recognise co-specific males as mates; and, b) Sexual selection: wing pigmentation is a sexually selected trait, favoured by male-male interactions and/or female choice. The evidence produced by single-species studies has lent support to the sexual selection hypothesis but given the chance that the mate recognition hypothesis may also apply (e.g. sympatry is common in this family members, some hybrids have been observed, among others evidence sets) a program of study that addresses both hypotheses is needed. We have investigated a number of mutually exclusive predictions in five calopterygids: *Calopteryx haemorrhoidalis, C. virgo, C. splendens, Hetaerina americana* and *H. vulnerata*. Our results indicate that: a) levels of pigmentation vary considerably within populations for all species; b) compared to males with less pigmentation, more pigmented males are more constantly chosen as mates by females or have a higher mating success, live longer, are less parasitised, and maintain territories for longer periods; and, c) pairs of species occurring in sympatry were not significantly different from each other in pigmentation patterns compared to those species occurring in allopatry. These results coincide with a sexual selection framework and are not predicted by the mate recognition hypothesis. It seems likely to ascribe sexual selection as the main selective pressure driving the maintenance of pigmentation in the Calopterygidae.

Posters

12.8P

BIOMETRICAL AND QTL ANALYSIS OF GENETIC VARIATION IN MALE COURTSHIP SONG CHARACTERS IN *DROSOPHILA VIRILIS*

Susanna Huttunen, Jouni Aspi

Department of Biology, P. O. Box 3000, 90014 University of Oulu, Finland

We analysed the inheritance of two male courtship song characters, number of pulses in a pulse train (PN), and length of a pulse train (PTL) in *Drosophila virilis*. Biometric analyses of song differences among 16 crosses over three generations (parental and reciprocal F1, F2, and backcrosses) were performed using two different approaches. The joint scaling test revealed significant additive and dominance components, and also significant additive interaction between maternal and progeny genotypes. In addition, planned comparisons (contrast analyses of variance) between different generations revealed significant Y chromosomal and transient maternal factors and their interactions, with all other factors contributing to differences in the means of song characters. These results suggest that the genetic basis of courtship song characters in *D. virilis* is primarily of autosomal polygenic nature, with small but significant Y chromosomal and nonchromosomal maternal effects. QTL-analysis was performed with 520 F2 males using a recombination linkage map constructed for 26 microsatellite markers. Single marker analysis showed two adjacent microsatellite markers on the 3rd chromosome, msat19 and vir84 to explain most of the variation both in PN and PTL (13.8%-12.4% and 9.9%-6.5%, respectively). Composite interval mapping analysis revealed significant QTLs affecting PN, located on the X and 2nd 3rd and 4th chromosome of *D. virilis*, while variation in PTL was most likely attributed to a single QTL located on chromosome 3 at the same position as the QTL affecting PN. The effects of QTLs were mainly additive. Dominance was observed only in QTL on the 3rd chromosome with a major effect on differences between the parental strains both in PN and PTL (31.8% and 49.1%, respectively).

12.9P

INFLUENCE OF THE COMPLEX COURTSHIP ON THE FEMALE ASSORTMENT AND THE NUMBER OF MATINGS IN TWO GRASSHOPPER SPECIES OF THE *CHORTHIPPUS ALBOMARGINATUS*-GROUP

[1]V. Y. Vedenina, [2]O. von Helversen

[1]Institute for Information Transmission Problems, Russian Academy of Sciences, Bolshoi Karetnyi per. 19, Moscow 127994, Russia

[2]Institute for Zoology II, University of Erlangen-Nuernberg, Staudtstrasse 5, 91058 Erlangen, Germany

Two closely related species *Chorthippus albomarginatus* and *C. oschei*, which hybridise in a contact zone on the territory of Ukraine and Moldova, have similar calling songs but extremely different and elaborate courtship songs. Choice mating experiments showed assortative mating between the species: the number of conspecific copulations in different experimental groups varied within a range of 78-91 %. During courtship, not only acoustic but also visual and olfactory cues are known to be of importance. To study the influence of different courtship components on assortative mating in *C. albomarginatus* and *C. oschei*, we conducted choice mating experiments on operated individuals. Elimination of the acoustic component (cutting of the male elytra) had the most crucial effect: there was not only a decrease in female selectivity but also a significant (5-7 times) reduction in the number of matings, although the muted males courted and made copulation attempts as eagerly as the intact males. We suggest that in *C. albomarginatus*-group, the elaborate courtship song plays an extremely important role in the stimulation of female to mate and influences the number of female matings. The evolution of male trait and female preference in the *C. albomarginatus*-group may be faster than in other grasshopper species due to a different mating strategy. A long and frequent courting of the competing males on the one hand, and frequent matings of females on the other hand, may facilitate female choice and favour competition among males similar to a "lek"-situation.

12.10P

A CHANGE IN A SINGLE SONG CHARACTER MAY BREAK SEXUAL ISOLATION

Mari Saarikettu, Jaana O. Liimatainen, Anneli Hoikkala

University of Oulu, P.O.Box 3000, 90014 Oulu, Finland

Drosophila montana and *D. lummei* are two partly sympatric species of *D. virilis* group. Interspecific courtships between these species are quite common in the wild, but they have never been observed to lead in copulation either in wild or in laboratory. We show here that sexual isolation between the species can be broken by playing *D. montana* females simulated courtship song with species-specific song characters, when the female is courted by a mute (wingless) *D. lummei* male. Even a change in a single song character (interpulse interval) raises significantly females' acceptance level. The study gives direct evidence on the role of acoustic cues in maintaining sexual isolation between closely related species. It also shows that the song characters playing a role species recognition may be different from those playing a role in sexual isolation.

Symposium 13

Geographical parthenogenesis and polyploidy

Organisers: Koen Martens & Peter Van Dijk

Roger Stevens Lecture Theatre 20

09.20 – 09.50	**Van Dijk, P. J.** Geographic parthenogenesis in higher plants
09.50 – 10.20	**Martens, K.** Geographic Parthenogenesis in animals: a review
10.20 – 11.00	**Coffee**
11.00 – 11.20	**Aguin-Pombo, D.** Origin and advantages of multiple clones of *Empoasca* like leafhoppers in the Madeira archipelago. Geographical patterns of parthenogenesis within an island escale
11.20 – 11.40	**Meirmans, P. G.** The distribution areas of sexual and asexual dandelions suggest postglacial recolonisation routes for which there is only scarce genetic evidence
11.40 – 12. 00	**Haag, C. R.** Coexistence of cyclical parthenogenetic and obligate parthenogenetic *Daphnia pulex* in a metapopulation
12.00 – 12.20	**Kapralov, M. V.** The Ural Mountains as a model system for studying South-North differentiation in sexuality and polyploidy, exemplified by the Nodding Saxifrage (*Saxifraga cernua*)
12.20 – 12.40	**Lamatsch, D. K.** Monophyletic origin of the triploid clones of the Amazon Molly, *Poecilia formosa*
12.40 – 14.00	**Lunch**

Invited talks

13.1

GEOGRAPHIC PARTHENOGENESIS IN HIGHER PLANTS

Peter J. Van Dijk

Netherlands Institute of Ecology, Boterhoeksestraat 48, 6666 ZG Heteren, The Netherlands

More than 25 years ago Bierzychudek's (1987) influential review on Geographic Parthenogenesis (GP) in plants was published. Since then many new studies have appeared. New insights in the genetic control of apomixis suggest that common ancestry of apomixis in related taxa is possible. It is therefore important to use phylogentically independent cases in the analysis of the geographic distribution patterns. In angiosperms almost all apomicts are polyploid, but most polyploids are sexual. If the distribution patterns of sexual polyploids differ in a similar way from sexual diploids as those of apomictic polyploids do, polyploidisation is a likely explanation for GP. So far nearly all cases of GP come from the Northern Hemisphere. The few studies from the tropical regions and from the Southern Hemisphere also suggest GP. Comparative studies (e.g. latitudinal and altitudinal gradients; macro- and micro-climate gradients) can help to understand the underlying causes of GP. Phylogeographic studies can give insight in the history of the today's geographic distributions. Molecular fingerprinting can identify wide- spread clones that are candidates for general-purpose-genotypes.

13.2

GEOGRAPHIC PARTHENOGENESIS IN ANIMALS: A REVIEW

K. Martens

Royal Belgian Institute of Natural Sciences, Freshwater Biology, Vautierstraat 29, 1000 Brussels, Belgium

Geographical parthenogenesis was first reported in animals under that name by Vandel (1928), who found that incidence of males in the terrestrial Isopod *Trichoniscus* in Europe decreased towards the north. A partial revision of GP in animals was offered by Suomolainen (1969), but several other patterns of differential distributions between reproductive modes have since been documented. Such distrbutions can be overlapping in the entire area, in part of the area or can be discrete. They can have ecological (differential tolerance, for example different degrees of disturbence, or xeric gradients), historical (different colonization rates after the retreat of the glaciers) or genetic (through hybridisation) causalities. Drivers behind the differential distributions can be a mixture of abitic factors, encompassed in latitude and altitude, or biotic interactions. An example of the latter is the ostracod *Cytherissa lacustris*, which is sexual in lagoons associated with the ancient Lake Baikal, but fully asexual in the rest of the Holarctic. Several theoretical and empirical models attempt to explain at least part of the observed patterns of GP and these are here reviewed.

Contributed talks

13.3

ORIGIN AND ADVANTAGES OF MULTIPLE CLONES OF *EMPOASCA* LIKE LEAFHOPPERS IN THE MADEIRA ARCHIPELAGO. GEOGRAPHICAL PATTERNS OF PARTHENOGENESIS WITHIN AN ISLAND SCALE

[1]N. Freitas, [2]**D. Aguin-Pombo**

[1]*University of Madeira, Campus da Penteada, 9000-390 Funchal, Madeira, Portugal*

[2]*Centre of Studies for Macaronesia, Campus da Penteada, 9000-390 Funchal, Madeira, Portugal*

Parthenoforms have greater colonisation ability than bisexual forms because only one individual is necessary to start a new population. Therefore, in particular habitats such as oceanic islands, asexual species can be in advantage in colonising and establishing new populations. Recently three morphologically distinct thelytokous forms similar to *Empoasca* leafhoppers have been reported from Madeira Island and these are the only cases of true parthenogenesis known within more than 600 species of this worldwide-distributed genus. In order to understand what promotes asexual reproduction in oceanic islands we addressed two main questions: (1) what is the origin of these parthenoforms? and (2) do asexual and their corresponding bisexual forms within these small islands have similar patterns of ecological requirements and distribution than those predicted in geographic parthenogenesis? After two years of extensive sampling, differences in host plant association and distribution between bisexual and sexual forms but also among clones were found. An analysis of the chromosome numbers showed that two clones are triploids, probably originated as the result of more than one hybridisation event between colonising bisexual species, while the third clone is diploid and may have arisen from a single parental species with latent parthenogenetic tendencies. Since parthenogenesis is an extremely rare phenomenon within the genus *Empoasca* and to a greater extent in the whole Auchenorrhyncha suborder, it is hypothesised that parthenogenesis was originated within these islands. Once an asexual form is originated, the relaxing selective pressures of these vacant enemy free insular habitats will facilitate their establishment increasing island diversity.

13.4

THE DISTRIBUTION AREAS OF SEXUAL AND ASEXUAL DANDELIONS SUGGEST POSTGLACIAL RECOLONISATION ROUTES FOR WHICH THERE IS ONLY SCARCE GENETIC EVIDENCE

Patrick G. Meirmans, Hans (J.) C. M. Den Nijs, Peter H. van Tienderen

University of Amsterdam, Kruislaan 318, 1098 SM, Amsterdam, The Netherlands

Dandelions (*Taraxacum* sect. *Ruderalia*) come in two flavors: sexually reproducing diploids and asexually reproducing triploids. The triploid apomicts are found almost in all parts of Europe, except for the Northernmost parts. The diploid sexuals however are restricted to the southern parts of western and central Europe, where they often co-occur with triploids in mixed populations. The distribution of diploid dandelions in this area shows a clearly disjunct pattern. Diploids are present in the larger part of France and in the Balkan, but in between these two areas, in southern Bavaria and Tirol, they are entirely lacking, even though the triploids are very common. This pattern has been explained to be a result of postglacial recolonization from two refugia; one in Spain and one in the Balkan. This recolonization hypothesis leads to the expectation of genetic differentiation between the western and eastern diploid distribution areas. We examined the genetic diversity within and among the two diploid distribution areas using both chloroplast RFLP's and microsatellites, sampling from diploid, triploid and mixed diploid/triploid populations. Almost all genetic variation was shared between the two distribution areas and also between the ploidy levels (low Fst-values), although the differentiation was significant. The diploid sexuals and triploid apomicts showed comparable levels of genetic differentiation between the Eastern and Western distribution areas. This provides further evidence for ongoing gene-flow between the two ploidy levels. However, the data shows that the division of the diploid distribution area in a Western and an Eastern part is not due to postglacial colonization patterns.

13.5

COEXISTENCE OF CYCLICAL PARTHENOGENETIC AND OBLIGATE PARTHENOGENETIC *DAPHNIA PULEX* IN A METAPOPULATION

Christoph R. Haag, D. Ebert

University of Fribourg, Ecology and Evolution, Chemin du musée 10, 1700 Fribourg, Switzerland and Tvärminne Zoological Station, 10900 Hanko, Finland

Daphnia pulex can either reproduce by cyclical parthenogenesis or by obligate parthenogenesis, and the frequency of obligate parthenogenesis increases with latitude. This pattern suggest that the relative fitness of obligate parthenogens relative to cyclical parthenogens increases with latitude. In Europe, the two forms coexist in the archipelago of southern Finland, where they occur in a metapopulation. To investigate the relative fitness of the two forms, we compared their competitive ability in several environments and estimated their resting-egg production. Obligate parthenogens had a much higher resting-egg production, which may be due to the fact that in obligate parthenogens resting-egg production is asexual and therefore does not require the prior production of males. This could indicate that obligate parthenogens are better dispersers than cyclical parthenogens, because resting-eggs are also the dispersal stages. Competitive ability, on the other hand, seemed to be highly dependent on the environment. In some cases, obligate parthenogens outcompeted cyclical parthenogens, and in some cases the outcome of competition was reversed. This might be explained by the fact, that certain environments induce male production in the cyclical parthenogenetic form, slowing down their population growth and thus reducing their competitive ability. Moving from south to north the growing season gets shorter and production of resting-eggs becomes more important. This may be one of the factors contributing to geographic parthenogenesis in *D. pulex.*

13.6

THE URAL MOUNTAINS AS A MODEL SYSTEM FOR STUDYING SOUTH-NORTH DIFFERENTIATION IN SEXUALITY AND POLYPLOIDY, EXEMPLIFIED BY THE NODDING SAXIFRAGE (*SAXIFRAGA CERNUA*)

[1]**M.V. Kapralov,** [2]T.M. Gabrielsen, [1]I. E. Sarapultsev, [3]N. A. Kutlunina, [3]O. S. Dymshakova, [2]C. Brochmann

[1]*Institute of Plant and Animal Ecology, RAS, 8 Marta street, 202, 620144 Ekaterinburg, Russia*

[2]*National Centre for Biosystematics, Natural History Museums and Botanical Garden, University of Oslo, P.O. Box 1172 Blindern, N-0318 Oslo, Norway*

[3]*Department of Botany, Urals State University, Lenin Avenue, 51, 620083 Ekaterinburg, Russia*

The Nodding Saxifrage, *Saxifraga cernua* L., is characterized by considerable variation in sexuality and ploidal level throughout its enormous distribution area, which includes the entire Arctic and some mountain outposts southwards. The distribution area in the Ural mountains appears as a narrow tongue stretched southwards from the circumpolar area for more than 1000 km. Our aims are to investigate reproductive and ploidal variation along the south-north gradient in this arctic-alpine model system. The Ural populations contain plants with at least three different ploidal levels and exhibit in microcosm the patterns of reproductive variation observed in the species as a whole: from purely asexual reproduction via bulbils to a significant role of sexuality. There is a clear relationship between chromosome number and sexuality: plants with $2n = 24$ produce more flowers per shoot and more fertile pollen than plants with $2n = 36$ and $2n = 48$, irrespective of the geographic origin of the population. The expected trend of decreasing sexuality and increasing ploidy level towards higher latitudes is, however, blurred in this regional population mosaic, which probably is highly influenced by the complex mountain reliefs and glaciation history of the Urals. Currently we use molecular markers (AFLPs) to assess the relationships among populations and potential trends in their patterns of clonal diversity.

13.7

MONOPHYLETIC ORIGIN OF THE TRIPLOID CLONES OF THE AMAZON MOLLY, *POECILIA FORMOSA*

[1]**Dunja K. Lamatsch**, [2]Kathrin P. Lampert, [3]Jörg T. Epplen, [1]Manfred Schartl

[1]*Department of Physiological Chemistry I, University of Wuerzburg, Biozentrum, Am Hubland, 97074 Wuerzburg, Germany*

[2]*University of Texas at Austin, Department of Integrative Biology, Austin, Texas, 78712, USA*

[3]*Department of Molecular Human Genetics, University of Bochum, 44801 Bochum, Germany*

The gynogenetic fish *Poecilia formosa* is a model system for the study of the evolution of sex, because the benefits and disadvantages of asexual reproduction can be evaluated and compared to the more common situation of sexual reproduction. *P. formosa* is an all-female species reproducing clonally but needing sperm of closely related sexual species to trigger the onset of embryonic development from the diploid oocyte nucleus. Usually male genetic material is excluded from the oocyte and does not contribute to the offspring's genotype. Paternal leakage is nevertheless possible. This incorporation of fresh genetic material is discussed as a possibility to overcome the accumulation of negative mutations predicted for clonal organisms (Muller's ratchet). Incomplete exclusion of the paternal chromatic material leads to host species derived microchromosomes (Schartl et al., Nature 1995). Using microdissection, we have isolated the microchromosome and are analysing its gene content. Alternatively, the entire sperm DNA is included in the diploid oocytes thus leading to triploid individuals. Paternal introgression, in particular through the formation of triploids was of major scientific interest because two important questions arose: are triploids genetically more variable than diploids and what is the major source of clonal variability, is it mutation or multiple introgression events? Earlier studies yielded conflicting results concerning the amount of genetic variation in triploids and diploids. Multilocus fingerprints and three microsatellite loci were used in this study to determine genetic variability in diploid and triploid *P. formosa*. While on the one hand multilocus fingerprints demonstrated a high degree of genetic variability in triploids, on the other hand, microsatellites that are highly variable among diploid lineages showed a monophyletic origin of triploids in *P. formosa*. Thus, while triploidy is a very efficient means of introducing fresh genetic material, it is an extremely rare event.

Posters

13.8P

NO NEED FOR SEX? EVOLUTION WITHOUT RECOMBINATION IN A SPECIOSE GROUP OF SOIL INVERTEBRATES

M. Heethoff, M. Laumann, M. Maraun, R. A. Norton

Technische Universitaet Darmstadt, Institut fuer Zoologie, Schnittspahnstrasse 3, 64287 Darmstadt, Germany

Recombination is assumed to be the main advantage of sexual reproduction. Organisms without recombination (asexuals) occur as terminal taxa, do not radiate and are doomed to extinction. There are only two well studied exceptions: the bdelloid rotifers and the darwinulid ostracods. Both are ancient and there is evidence for radiation without biparental reproduction in both groups. A third group, containing even more parthenogenetic species than do rotifers and ostracods, are the oribatid mites (Acari, Oribatida). They are mainly soil living animals with about 9000 described species. The first fossil records are from Devonian sediments. Hundreds of obligate parthenogenetic species evolved as independent clusters. Oribatid mites appear to have holokinetic chromosomes, and inverted meiosis has been inferred. In parthenogens, diploidy is restored by terminal fusion, which is functionally equivalent to apomictic cloning. With this lack of recombination, homologous alleles should diverge over time and heterozygosity should be high. We analysed the two alleles for the hsp82 gene of different sexual and asexual species from a wide range of oribatid mite taxa. Phylogenetic reconstruction of the two alleles formed two clusters with heterozygous specimens having one allele from each of the two clusters indicating that the divergence of hsp82 was before the radiation of oribatid mites. Ancient loss of sexuality is also documented for two monophyletic asexual groups of oribatid mites using DNA sequences of the mitochondrial gene for cytochrome oxidase I. Specimens from different continents were analysed. Genetic variation was high and saturated with maximum nucleotide distances of 136% for Camisiidae and 157% for Trhypochthoniidae. These groups presumably have existed since the breakup of Pangea (200 myrs). Our data document that asexual oribatid mites are ancient and possibly the most extraordinary of the "evolutionary scandals" with several asexual speciose clusters. The evolution of the whole group of oribatid mites (and perhaps all acariform mites) without intrachromosomal recombination is another "scandal", at the moment unique in the animal kingdom.

13.9P

GENETICS OF SEXUAL AND PARTHENOGENETIC REPRODUCTION IN *VENTURIA CANESCENS* (HYMENOPTERA)

I. Mateo-Leach, L. Beukeboom, L. van de Zande

Evolutionary Genetics, Biological Centre, University of Groningen, Kerklaan 30, NL-9751 NN Haren, The Netherlands

Biologists have studied over years why most of the species reproduce sexually while others reproduce asexually, particularly since asexual reproduction in theory has a two-fold advantage. >From a genetic perspective, asexuals spread their genes twice as fast as sexuals do. While several ecological studies are carried out to elucidate the short-term benefits of sexual reproduction, very little attention is being paid to the genetic regulation of both reproductive modes, which is essential for understanding how sex is maintained. Our model animal for this research is *Venturia canescens* (Gravenhorst) (Hymenoptera: Ichneumonidae). It is a solitary koinobiont endoparasitoid of pyralid moths. Both arrhenotokous (sexual) and thelytokous (asexual, not *Wolbachia*-induced) modes of reproduction occur sympatrically. We recently discovered that crosses between arrhenotokous males and thelytokous females are possible and lead to insemination of the thelytokous female. If this leads to recombinant fetile offspring, it opens up the possibility to study for the first time the genetics of parthenogenesis in a higher animal.

13.10P

BREAKDOWN OF SELF-INCOMPATIBILITY CLOSE TO THE NORTHERN RANGE MARGIN IN THE WINDPOLLINATED PERENNIAL HERB *PLANTAGO MARITIMA*

Emil V. Nilsson, Kirsten Wolff, Jon Ågren

Uppsala University, Department of Plant Ecology, Villav. 14, 752 36 Uppsala, Sweden

In flowering plants, selfing has repeatedly evolved from outcrossing through the loss of self-incompatibility. This evolutionary transition has a strong influence on the distribution of genetic diversity within and among populations, and will affect the conditions for the maintenance of sexual polymorphism. We estimated the outcrossing rate of hermaphrodite plants in five populations of the gynodioecious perennial herb *Plantago maritima* along a latitudinal gradient across Sweden and Finland. The estimates were based on variation at five polymorphic microsatellite loci in maternal progeny groups. The results indicate that the southern populations are fully outcrossing, which is consistent with previous reports of strong self-incompatibility in this species. In contrast, hermaphrodites in the northern populations self-fertilize to a considerable extent. Reproductive assurance may have contributed to the evolution of self-compatibility in locally isolated and sparse populations at the northern range margin of *P. maritima*.

13.11P

POPULATION HISTORY AND BIOGEOGRAPHY OF *EUCYPRIS VIRENS*, AN OSTRACOD SPECIES WITH GEOGRAPHIC PARTHENOGENESIS

I. Schön

Royal Belgian Institute of Natural Sciences, Freshwater Biology, Vautierstraat 29, 1000 Brussels, Belgium

The non-marine ostracod species *Eucypris virens* shows a typical pattern of geographic parthenogenesis, with a restricted distribution of sexuals around the Mediterranean, and with asexual populations occurring throughout the whole of Europe. Phylogenetic reconstructions from ITS1 sequence data (Schön et al. 2000) result in numerous equally parsimonious trees, because sexual and asexual lineages are closely entangled. Network constructions and nested clade analyses are powerful statistical tools to resolve relationships at the intraspecific level. Here, they are employed to nuclear ITS1 and mitochondrial COI sequence data from European populations of *E. virens* to test whether range expansion of asexuals after the ice-ages is still detectable or has meanwhile been overwritten by recent gene flow between populations. This type of analyses will also provide a much finer resolution of the geographic and genetic relationships between sexual and asexual lineages of this species.

Symposium 14

Positive selection and adaptive trait genes

Organisers: Christian Schlötterer & Diethard Tautz

Roger Stevens Lecture Theatre 21

09.20 – 09.50	**Nachman, M. W.** The genetic basis of adaptive melanism in pocket mice
09.50 – 10.20	**Stephan, W.** Multi-locus approaches to distinguish the effects of demography, substructure and selection in *Drosophila*
10.20 – 11.00	**Coffee**
11.00 – 11.20	**Anderson, T. J. C.** Drug treatment and hitchhiking in SE Asian malaria parasites
11.20 – 11.40	**Hasselmann, M.** Distribution of nucleotide polymorphisms, recombination rate and nonsynonymous sites at a locus under strong overdominance selection
11.40 – 12. 00	**Ihle, S.** Searching for genes involved in environmental adaptations in mouse populations
12.00 – 12.20	**Wiener, P.** Patterns of diversity near a selected locus in cattle
12.20 – 12.40	**Emerson, B. C.** Origin and maintenance of a broad-spectrum disease resistance locus in *Arabidopsis*
12.40 – 14.00	**Lunch**

Invited talks

14.1

THE GENETIC BASIS OF ADAPTIVE MELANISM IN POCKET MICE

M. W. Nachman

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA

Identifying the genes underlying adaptation is a major challenge in evolutionary biology. One approach to this problem is to choose ecologically important traits for which candidate genes are available, and then to screen these genes for associations with the phenotype of interest. Here I describe the molecular changes underlying adaptive coat color variation in a natural population of rock pocket mice, *Chaetodipus intermedius*. Rock pocket mice are generally light-colored and live on light-colored rocks. However, populations of dark (melanic) mice are found on dark lava, and this concealing coloration provides protection from avian and mammalian predators. Association studies using markers in candidate pigmentation genes revealed four mutations in the melanocortin-1-receptor gene, *Mc1r*, that appear to be responsible for adaptive melanism in one population of lava-dwelling pocket mice. Linkage disequilibrium decays rapidly near *Mc1r*, suggesting that a genomic scan for selection would have missed this gene, despite its clear importance in adaptive evolution. Interestingly, other melanic populations of these mice on different lava flows show no association with *Mc1r* mutations, indicating that adaptive dark color has evolved independently in this species through changes at different genes.

14.2

MULTI-LOCUS APPROACHES TO DISTINGUISH THE EFFECTS OF DEMOGRAPHY, SUBSTRUCTURE AND SELECTION IN *DROSOPHILA*

Wolfgang Stephan

Department of Biology II, University of Munich

Demography, population substructure and natural selection have been recognized for their important roles in shaping patterns of nucleotide variability. To investigate their relative effects in *D. melanogaster*, we screened DNA sequence variation in a putatively ancestral African and a derived European population. Surpringly, there is strong evidence for a recent size expansion in the African population (but little indication of the action of past natural selection). In contrast, signatures of positive directional selection were found in the European population, such as a reduction of variation at various regions along the genome and elevated levels of differentiation at these low-variation loci. A similar study (using samples from more than 15 locations throughout Southeast Asia) was conducted in *D. ananassae* to identify the center of diversity of this highly sub-structured species and to detect geographic patterns of local adaptation.

Contributed talks

14.3

DRUG TREATMENT AND HITCHHIKING IN SE ASIAN MALARIA PARASITES

[1]**Tim J. C. Anderson**, [1]Shalini Nair, [1]Jeff T. Williams, [2]Alan Brockman, [2]Francois Nosten

[1]*Southwest Foundation for Biomedical Research, San Antonio, TX 78245, USA*

[2]*Shoklo Malaria Research Unit, Mae Sot, Tak, Thailand*

Malaria parasites provide excellent opportunities for studying the genomic effects of selection in a recombining eukaryote, since the rapid spread of resistance to multiple drugs has been well documented, the full genome sequence is now available, and haplotypes are easily generated. We examined microsatellite variation around dihydrofolate reductase (*dhfr*) (Chr 4). Specific point mutations in (*dhfr*) result in resistance to pyrimethamine, and resistance to this drug has spread rapidly in SE Asia. We genotyped microsatellites distributed across Chr 4 in parasites from a Thai location. We observed minimal microsatellite length variation for 12kb (0.7cM) flanking resistant dhfr alleles and reduced variation for ~100kb (6cM). Furthermore, we found the same or similar microsatellite haplotypes flanked resistant (*dhfr*) alleles sampled from 11 parasite populations in five SE Asian countries indicating recent invasion of a single lineage of resistant alleles in locations 2000km apart. Microsatellites flanking resistant alleles also showed skewed allele distributions and elevated LD consistent with expectations of hitchhiking. Three features of these data are of especial interest: 1) Pyrimethamine resistance is assumed to have evolved multiple times, since the genetic basis is simple and resistance can be selected easily in the laboratory. Yet our data indicate a single origin of resistance alleles over a large region of SE Asia. 2) The wide valley (~6cM) of reduced variation around (*dhfr*) provides "proof-of-principle" that genome scans may be an effective way to locate genes for adaptive traits in this organism, despite high recombination rates 3) The width of the selective valley is consistent with predictions based on independent measures of recombination, mutation and selection intensity. Scanning the malaria genome for selection may provide both an effective way to locate resistance genes and an opportunity to study the dynamics of selective events that have occurred recently or are currently in progress.

14.4

DISTRIBUTION OF NUCLEOTIDE POLYMORPHISMS, RECOMBINATION RATE AND NONSYNONYMOUS SITES AT A LOCUS UNDER STRONG OVERDOMINANCE SELECTION

Martin Hasselmann, Martin Beye

Martin Luther Universität Halle/Wittenberg, Institut für Zoologie, Biozentrum,
Weinberg Weg 22, 06120 Halle, Germany

Selection has major effects on the distribution of nucleotide polymorphisms in populations and these signatures should be detectable. Here we report the study of alleles and linked genomic regions of the complementary sex determiner (*csd*), a locus under strong overdominant selection in which homozygotes have zero fitness, heterozygotes develop into females and hemizygotes differentiate into males. Our molecular analyses show diverged alleles segregating in populations. Signatures of positive selection within the gene are given by striking nucleotide polymorphisms with an excess of nonsynonymous over synonymous substitutions per site in different parts of the protein. Signatures of selection are also found in linked loci. Nucleotide diversity strongly increase within the proximity of the selected locus. However, polymorphisms rapidly decline in less than 50 kb distance, indicating the strong influence of recombination. Measurement of recombination rate shows an increased recombination rate in close proximity of the locus, suggesting that recombination rate is positive selected uncoupling *csd*-alleles from the rest of the genome. Our empirical results suggest that signatures of elevated polymorphisms are detectable only in short physical distance to the selected locus and are strongly influenced by recombination.

14.5

SEARCHING FOR GENES INVOLVED IN ENVIRONMENTAL ADAPTATIONS IN MOUSE POPULATIONS

Sonja Ihle, Diethard Tautz

Universitaet zu Koeln, Institut fuer Genetik, Abteilung für Evolutionsgenetik, Weyertal 121, 50931 Koeln

Microsatellite screening at multiple loci in different house mouse populations can be applied to reveal the evolutionary forces acting on genomic regions after population divergence. In an attempt to devise a systematic screen for genes involved in environmental adaptations, we have so far screened 82 microsatellite markers in five wild caught populations, two of the eastern house mouse (*Mus musculus*) from the Czech Republic and Kasakhstan and three of the western house mouse (*Mus domesticus*) from Germany, France and Cameroon. The microsatellite loci were in close linkage to candidate genes that could play a role in environmental or social interaction and were therefore likely to be affected by recent selective forces. By multiple population comparisons which also included different evolutionary divergence times between the populations we were able to identify seven microsatellite loci that lost variability in single populations. Since microsatellites are considered to behave neutrally the loss of variability of a marker can be an indicator of a selective sweep event of a gene in close vicinity to the neutral marker.The genes that were linked to these microsatellites are known to play a role in different functions in the organisms such are microbial defense, olfactory receptors, interferon receptors, and genes involved in male sterility. This shows that this approach is potentially suitable to identify genes involved in adaptations, solely on the basis of the evolutionary signature that they leave in populations.

14.6

PATTERNS OF DIVERSITY NEAR A SELECTED LOCUS IN CATTLE

Pam Wiener, Deborah Burton, John L. Williams

Roslin Institute, Roslin, UK

This study explored patterns of genetic diversity near a locus known to have been under selection. The myostatin gene (GDF-8) has been shown to be associated with double muscling, a phenotype selected for in a number of cattle breeds. We examined population genetic parameters for microsatellite loci at varying distances from GDF-8 in double-muscled and non-double-muscled cattle breeds in order to assess patterns of diversity. A theoretical analysis was also performed to predict the patterns of diversity expected under different scenarios. We found differences in the patterns of heterozygosity, allele diversity and linkage disequilibrium between double-muscled and non-double-muscled breeds. However, there were some exceptions to the predicted patterns. These are discussed in light of the histories of the breeds and the potential for using microsatellite diversity for mapping trait genes in livestock populations.

14.7

ORIGIN AND MAINTENANCE OF A BROAD-SPECTRUM DISEASE RESISTANCE LOCUS IN *ARABIDOPSIS*

[1]Shunyuan Xiao, [1]**Brent C. Emerson**, [1]Kumrop Ratanasut, [1]Elisabeth Bent, [2]Carmel O'Neill, [2]Ian Bancroft, [2]John G. Turner

[1]School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK

[2]John Innes Centre, Norwich Research Park, Colney, Norwich NR4 7UH, UK

The broad-spectrum mildew resistance genes RPW8.1 and RPW8.2 define a unique type of plant disease resistance (R) genes and so far homologous sequences have been found in Arabidopsis thaliana only, suggesting a recent origin. In addition to RPW8.1 and RPW8.2, the RPW8 locus contains three homologues of RPW8, HR1, HR2, and HR3, which do not contribute to powdery mildew resistance. To understand the origin of the RPW8 locus, we isolated the syntenic RPW8 loci from *Arabidopsis lyrata*, and from *Brassica rapa* and *B. oleracea*. The *A. lyrata* locus contains four genes orthologous to HR1, HR2, HR3 and RPW8.2 respectively. Two syntenic loci have been characterized in *Brassica*, one contains three genes and is present in both *B. oleracea* and *B. rapa*, and the other contains a single gene and is detected in *B. rapa* only. All of the *Brassica* homologues are most homologous to HR3. Sequence analyses suggested that the RPW8 gene family in Brassicaceae originated from an HR3-like ancestor gene through a series of duplications and that RPW8.1 and RPW8.2 evolved from functional diversification through positive selection several millions of years ago. By examination of the sequence polymorphism of 32 *A. thaliana* accessions at the RPW8 locus and their disease reaction phenotypes, we further demonstrate that the polymorphic RPW8 locus, which controls a major sources of resistance to powdery mildew diseases, has been maintained in contemporary populations of *A. thaliana* by balancing selection for a benefit of resistance against a cost of resistance.

Posters

14.8P

PHENOTYPIC CHARACTERISATION AND QUANTIFICATION TO ZINC TOLERANCE OF *ARABIDOPSIS ARENOSA (BRASSICACEAE)*

Laurent Amsellem

Laboratoire de Génétique et Evolution des Populations Végétales, Bâtiment SN2, Université des Sciences et Technologies de Lille 1, F-59655 Villeneuve d'Ascq Cedex, France

Organisms able to tolerate high heavy metal contents in their environment have been an increasing interest field of research because of the leading adaptations concerned for living with such toxic substances. As a key species for such researches in plants, *Arabidopsis halleri halleri* (Brassicaeae) have shown to be constitutively tolerant to very high zinc concentrations in soils. Previous field observations suggest that a phylogenetically close species, *A. arenosa*, could also be tolerant to very high zinc contents in soils, and this adaptation could not be isolated for these two taxa in the genus *Arabidopsis*. As a first step toward a deeper look in the whole genus, our study focuses on the phenotypic characterisation of zinc tolerance of *A. arenosa*, for individuals taken from metalicollous populations (from Germany and Poland) - where it is met in sympatry with *A. halleri halleri* - and from others from a non-metalicollous site (from Slovakia). This work will allow (i) to characterise zinc tolerance for A. arenosa, (ii) to evaluate if tolerance met for *A. arenosa* is independent of the edaphic origin (metalicollous / non metalicollous) as for its closely relative *A. halleri halleri*, and (iii) to quantify and to compare its tolerance levels with the ones observed for *A. halleri halleri*. A second step toward a deeper knowledge about genetic determinism of heavy metal tolerance will be to determine if tolerance met for *A. arenosa* represents a homologous trait or an evolutionary convergence in comparison with the one observed for *A. halleri halleri*. Indeed, some molecular markers showed to co-segregate with the tolerance trait for progenies from interspecific crosses between *A. halleri halleri* and the close non-tolerant species *A. lyrata petraea*.

14.9P

NUCLEOTIDE POLYMORPHISM AND DIVERGENCE AT *FROST (FST)*: A GENE INVOLVED IN THE RESPONSE TO COLD SHOCK IN *DROSOPHILA*.

Carlos Arboleda-Bustos, Carmen Segarra

Universitat de Barcelona, Facultat de Biologia, Av .Diagonal 645,08028. Barcelona, Spain.

Cold acclimation and tolerance are adaptive characters that might be modulated by natural selection. Therefore, genes involved in cold resistance are good candidates to have suffered adaptive changes. Recently, one of these genes has been identified in *Drosophila melanogaster*. The *Frost (Fst)* gene is up-regulated during the period of recovery after a cold shock. This gene has been cloned and sequenced. The FST protein (278 amino acids long) has a stretch of proline residues and present the motif PEEST repeated several times. Here, we report a study on nucleotide polymorphism and divergence at *Fst* in *Drosophila*. Nucleotide variation in an approximately 1.5 kb fragment including this gene was analyzed in lines isolated from two natural populations of *D. melanogaster*: 13 lines were collected in Montemayor (Córdoba, south of Spain) and 11 in Sant Sadurni d'Anoia (Barcelona, Catalonia, northeast of Spain). These populations are not genetically differentiated at *Fst*. The total number of mutations detected was 16: 7 in noncoding sites, 2 synonymous and 7 nonsynonymous. Nucleotide diversity estimates for silent (noncoding plus synonymous), synonymous and nonsynonymous sites were 0.0024, 0.0054 and 0.0015, respectively. A significant excess of nonsynonymous polymorphism (or synonymous fixed differences) was detected by the McDonald and Kreitman test when *D. simulans* was used as the outgroup. Divergence at *Fst* has been analyzed between *D. melanogaster*, *D. simulans*, *D. mauritiana*, *D. yakuba* and *D. erecta*. The length of the coding region differed considerably between the species; it ranges from 278 codons in *D. melanogaster* to 340 in *D. simulans*. These differences in length are mainly due to differences in the number of the PEEST motifs.

14.10P

ADAPTIVE HITCH-HIKING SIGNATURE ON NEUTRAL GENETIC DIFFERENTIATION BETWEEN POPULATIONS.

[1]P. H.Garnier-Géré, [2]F. Austerlitz, [3]V. Lecorre, [1]A. Kremer

[1]INRA, Equipe de Génétique et d'Amélioration des arbres Forestiers, 69 route d'Arcachon, Cestas 33612, France

[2]Laboratoire Ecologie, systématique et évolution, Université Paris-Sud, UPRESA-CNRS 8079, Bat. 362, 91405, Orsay cedex , France

[3]INRA, Unité de Malherbologie et Agronomie, B.P. 86510, 21065 Dijon Cedex, France

Characteristic features of the hitchhiking process, including reduction of diversity around the selected locus and excess of high-frequency derived mutations, have been studied and used for testing departures from neutrality. The consequences of genetic hitchhiking on differentiation between populations at linked neutral loci have received however much less attention. The few existing models show that a substantial increase in differentiation can occur at neutral loci for low levels of migration and for recombination rates smaller than selection coefficients. These models are restricted to one selected locus and a small number of alleles, or to very few populations. Thus the question remains of the importance of hitchhiking effects in natural populations, where selection affects polygenic traits, and in the case of species with high migration rates. Using a simulation approach, we explore the evolution of the molecular differentiation at genes controlling an adaptive trait, and at surrounding neutral markers with increasing recombination rates, in a subdivided population. The trait is submitted to both stabilizing selection within population and diversifying selection between populations. We study the impact of the intensity of these two selective forces on the level of genetic hitchhiking. The results are discussed in the context of screening genomes in order to detect genes that have been submitted to selection.

14.11P

EVOLUTIONARY RATES OF PRIMATE X- AND Y-LINKED GENES

Dave T. Gerrard, Dmitry A. Filatov

School of Biosciences, The University of Birmingham, Edgbaston, Birmingham, B15 2TT

Sex chromosomes are thought to evolve from a pair of autosomes (proto-sex chromosomes) via cessation of recombination between the proto-X and proto-Y chromosomes and gradual genetic degeneration of the Y-linked genes. The degeneration of the non-recombining Y chromosome is probably due to the inability of the Y-linked genes to adapt to a changing environment (faster X hypothesis, Orr and Kim, 1998), or due to an accumulation of deleterious mutations on the Y chromosome (Rice, 1987, Charlesworth and Charlesworth, 2000). The faster X hypothesis predicts a faster accumulation of (adaptive) amino-acid substitutions in the X-linked genes, compared to the Y-linked genes, while the second hypothesis predicts a higher rate of (deleterious) amino-acid substitutions on the Y, compared to the X chromosome. Here we attempt to distinguish these two hypotheses using the estimates of evolutionary rates at the silent (Ks) and non-silent (Ka) sites in several newly sequenced homologous primate X- and Y-linked genes.

14.12P

A MULTI-LOCUS SURVEY OF *DROSOPHILA MELANOGASTER* X CHROMOSOME: DEMOGRAPHY AND NATURAL SELECTION SHAPED GENETIC VARIATION

Lino Ometto, Sascha Glinka, Sylvain Mousset, Wolfgang Stephan, David De Lorenzo

Department Biologie II, University of Munich, Luisenstrasse 14, D-80333 Munich, Germany

According to population genetics theory, demography and selection might play combined roles in shaping patterns of nucleotide variability. In the present study, we investigate the effects and the importance of these forces in the genome of *Drosophila melanogaster*. To increase the power of the analysis, we used a multi-locus survey of nucleotide diversity across the whole X-chromosome in a putatively ancestral African and a derived European population. We found evidence that demographic effects acted in both the derived European and, surprisingly, the ancestral African populations. Evidence for positive natural selection was on the other hand found only in the European sample, as indicated by (i) a large number of loci showing low levels of variation, and (ii) a significant excess of derived variants at the low-variation loci that are fixed in the European sample but rare in the African population. These results are consistent with the hypothesis that the European population has experienced frequent positive Darwinian selection, during its recent adaptation to new habitats. Our study shows the advantages of a genomic approach, over a locus-specific analysis, in disentangling demographic and selective forces.

14.13P

EVOLUTION AND ADAPTIVE SIGNIFICANCE OF THE ARYL HYDROCARBON RECEPTOR (AHR) IN ATLANTIC SALMON (*SALMO SALAR*) LIVING IN THE BALTIC SEA

Maria Hansson, Torbjörn von Schantz, Håkan Wittzell, Kerstin Persson

Lund University, Department of Animal Ecology, Solvegatan 37, SE-223 62 Lund, Sweden

The aryl hydrocarbon receptor (AhR) mediates the toxicity of several environmental contaminants e.g. 2,3,7,8-tetrachlorodibenzo-*p*-dioxin (TCDD) and other halogenated hydrocarbons in vertebrates. This receptor initiates the transcription of several biotransformation enzymes (e.g. CYP1A), which in turn are responsible for causing severe harm to biological tissues from the generation of excessive amounts of oxidative metabolites. The AhR-initiated transcription of the biotransformation enzymes ultimately leads to oxidative stress and severe cell damage, stressing the importance of the AhR in the resulting toxicity of environmental pollutants. Fishes are especially sensitive to organic environmental pollutants and most notably so during their early developmental stages when exposure can seriously disrupt vital life functions and ultimately cause death. Thus, since the exposure to environmental pollutants (e.g. PAHs, PCBs and dioxins) increase the levels of various biotransformation enzymes in the cells, measures of CYP1A induction is today generally recognized as an important biomarker of PAH and PCB exposure in fish. We have identified and isolated four functional AhR type 2 genes in the teleost fish Atlantic salmon (*Salmo salar*), a species native to the North Atlantic Ocean and the surrounding costal rivers. The presence of multiple AhR genes is probably a consequence of the genome duplications that occurred in the early evolution of fish and later also specifically in the salmonid lineage. Our study aims at investigating the evolution as well as adaptive significance and allelic variation of the AhR genes and its signalling pathways in salmon populations residing in the highly contaminated Baltic Sea. In addition to presenting the evolution of the AhR complex in Atlantic salmon, data from Real-Time analyses will be presented, giving estimates of the individual expression of the four AhR2 genes in relation to the expression of the CYP1A in adult Atlantic salmons sampled in the Baltic Sea.

14.14P

NATURAL SELECTION AT THE SELF-INCOMPATIBILITY LOCUS OF *ARABIDOPSIS LYRATA* (BRASSICACEAE)

E. M. Kamau, D. Charlesworth

Univeristy of Edinburgh, King's Buildings, West Mains Road, Edinburgh, EH9 3JT

Self-incompatibility (SI) is a widespread mechanism ensuring out-crossing in plant species. In *Arabidopsis lyrata* (Brassicaceae) the sporophytic SI system is controlled by two genes at the S-locus that code for male and female components of the recognition process. The stigma component of this system is the S-locus receptor kinase encoded by the SRK gene which has been shown to be necessary for determining SI reactions. Several SRK alleles and very high levels of diversity have been found in natural populations of *A. lyrata*. The mechanisms responsible for this polymorphism are unknown but population genetics theory predicts that SI alleles should be maintained in populations for very long times due to the action of frequency-dependent selection. Analyses of sequences of Brassica SRK alleles have identified regions that might be under positive selection. So far only the extra-cellular S-domain has been studied. Here, we test for evidence of balancing selection acting on the SRK gene: we study both the S-domain and also the intra-cellular kinase domain to explain the high polymorphism found at the locus. We expect that the high diversity observed in the intra-cellular kinase domain is not maintained by selection but rather as a result of linkage to the extra-cellular S-domain where specificity is determined.

14.15P

MICROPROPAGATION OF *RHODIOLA ROSEA L.*

Tasheva Krasimira, Zagorska Nedyalka

Institute of Genetics, 1113, Sofia, Bulgaria

The species *Rhodiola rosea L.* (Crassulaceae) is not wide spread. It grows in the Balkan, Rila, Pirin and Rhodopa up to 2600 m altitude. The plants contain biologically active substances - rosavin /2.1%/, salidrosid /0.8%/ etc. Therefore they are used in the medical practice against cancer and nervous diseases as well as in cases of decreased capacity for work. The purpose of this investigation was to elaborate an efficient method for in vitro propagation. Over 10 nutrient media have been tested. The most suitable of them efficiently favoring seed germination and regeneration from different explants have been identified. The MS + 2 mg/l zeatin and 0.2 mg/l IAA medium was found to be the optimum because 76.67% of the explants grown on it provided regenerants. Up to ten regenerants could be obtained from one explant. System for further efficient micropropagation was established allowing growth of up to 50 plants from an initial explant for 3 months. There are difficulties in rooting and adaptation of plants in vivo and markers are searched for overcoming this problem.

14.16P

MOLECULAR EVOLUTION AT THE WITHIN AND BETWEEN POPULATION LEVELS IN *ARABIDOPSIS THALIANA*: THE *FRIGIDA* GENE.

Valérie Le Corre, Lucile Jacquens, Fabrice Roux

UMR Biologie et Gestion des Adventices, INRA, BP 86510, 21065 Dijon cedex, France

Frigida is a major gene controlling flowering time and the response to vernalization in *Arabidopsis thaliana* (Johansson et al., 2000). Nucleotide variation at this gene was investigated within and among natural populations of *Arabidopsis* sampled in France and representing contrasted climatic conditions. Variation at the *Frigida* gene was compared with variation at molecular markers (microsatellites and Cleaved Amplified Polymorphic Sequences) randomly distributed across the genome. In accordance with previous results at the between population level (Le Corre et al., 2002), sequence variation at the *Frigida* gene was characterized by an excess of non-synonymous changes, mainly in the first exon, and the presence of numerous knock-out mutations (mostly small indels) throughout the gene. Similar patterns of within and among population structure were observed for nucleotide diversity at *Frigida* and allelic diversity at markers. A subset of the sampled populations were fixed or nearly fixed at all loci, whereas the other populations showed an unexpectedly high level of polymorphism, given the high rate of inbreeding in this species. Fst values calculated from nucleotide substitutions at *Frigida* and molecular markers were not significantly different. By constrast, the value of differentiation based on the presence or absence of knock-out mutations was higher, suggesting the action of local selection. The high level of polymorphism within population may be caused by several factors: out-crossing events, large numbers of migrants, fine-scale isolation-by-distance, or fine-scale local selection. To test these different hypotheses, about one hundred individuals were sampled along a transect within each of two populations. Variation at the *Frigida* gene and at molecular markers was assayed together with variation at quantitative traits including flowering time. Results of multilocus and spatial analyses are presented.

14.17P

Y CHROMOSOME EVOLUTION AND THE *SEX-RATIO* SYSTEM IN *DROSOPHILA SIMULANS*

[1]Catherine Montchamp-Moreau, [2]Anne Atlan

[1]*CNRS, UPR 9034, Populations Génétique et Evolution, avenue de la terrasse F91198 Gif-sur-Yvette*

[2]*CNRS, UMR 6553, Ecobio, Université Rennes 1, F35042 Rennes*

The *sex-ratio* trait, known in natural populations of several drosophila species, results from meiotic drive of the X chromosome against the Y chromosome. Males that express the trait produce strongly female-biased progeny. The emergence of *sex-ratio* X chromosomes is expected to lower the polymorphism of the Y chromosome through adaptative sweep of Y-linked suppressors, because a Y chromosome able to resist drive has a strong selective advantage over a sensitive Y. We addressed this question through the study of Y chromosomes sampled in natural populations of *Drosophila simulans*, a species where drive supressors have evolved and maintain a roughly equal sex ratio in populations even when driving X chromosomes are at high frequency. We found that the Y chromosomes were highly polymorphic with regard to their ability to suppress drive, thus suggesting that the evolution of sex-ratio systems could on t he contrary increase the polymorphism of the Y chromosome. However, sequence analysis of Y-linked genes did not revealed any variation among the suppressor Y chromosomes, which support the selective sweep hypothesis.

14.18P

NON-CODING DNA VARIATION ACROSS THE X-CHROMOSOME OF *DROSOPHILA MELANOGASTER*:

[1]Dorcas J. Orengo, [2]Aleksandra Gondek, [1]Montserrat Aguadé

[1]*Universitat de Barcelona, Diagonal 645, 08028 Barcelona, Spain*

[2]*Universitat de Barcelona, Diagonal 645, 08028 Barcelona, Spain / Institute of Nature Conservation, Polish Academy of Science, Krakow, Poland*

Surveys of nucleotide variation in natural populations of *Drosophila melanogaster* have shown that X-chromosomal regions generally exhibit a lower level of variation in non-African than in African populations. Although this observation is consistent with a stochastic loss of variation during the out-of-Africa expansion of the species, it could be also explained by selective sweeps associated with its adaptation to temperate zones. Multilocus surveys of variation can shed light on the relative importance of demographic and selective events, since only the former are expected to affect similarly all regions studied. Over 100 non-coding regions distributed across the X chromosome were chosen for the present study. Sequences for a medium-sized sample from a Spanish *D. melanogaster* population and from a single strain of *D. simulans* were obtained. Nucleotide variation within and between species was estimated for each region, and these estimates compared among regions. Different summary statistics and tests were used for comparing intraspecific patterns of variation. These analyses allowed us to identify some outlier regions that we consider good candidates for their variation having been shaped by natural selection. In order to contrast the putative role of positive selection in these outlier regions, a more detailed study has already been persued around a region (located in band 3C) that exhibited one of the lowest levels of polymorphism and no parallel decrease of divergence.

14.19P

QTL-LINKED MICROSATELLITE LOCI AS INDICATORS OF ADAPTIVE POPULATION DIFFERENTIATION IN BROOK TROUT (*SALVELINUS FONTINALIS*) FROM GROS MORNE NATIONAL PARK, NEWFOUNDLAND, CANADA.

[1]Jocelyn Poissant, [2]Thomas W. Knight, [1]Moira M. Ferguson

[1]University of Guelph, Department of Zoology, Guelph, Ontario, Canada, N1G-2W1

[2]Gros Morne National Park of Canada, P.O. Box 130, Rocky Harbour, NL, Canada, A0K-4N0

We determined the genetic population structure of brook trout (*Salvelinus fontinalis*) from two ecologically distinct habitats (highlands and lowlands) in and around Gros Morne National Park, Newfoundland, Canada. Marked differences in water temperature and length of the growing season between the two habitats likely expose fish to divergent natural selection for growth and stress tolerance traits. We tested the hypothesis that microsatellite loci known to be linked to quantitative trait loci (QTL) for body size and/or upper thermal tolerance in other salmonid species (rainbow trout, *Oncorhynchus mykiss* and Arctic charr, *Salvelinus alpinus*) are better predictors of adaptive population differentiation than loci with no known associations with similar QTL. Incongruence between the patterns of population relationships derived from the different sets of microsatellite loci would suggest that variation in QTL-linked markers might mirror heritable variation in adaptive traits. To our knowledge, this study represents one of the first attempts to use QTL-linked microsatellite loci to detect adaptive differentiation in natural populations.

14.20P

NUCLEOTIDE VARIATION ACROSS A LONG STRETCH OF NON-CODING DNA IN A HIGHLY RECOMBINING REGION OF *DROSOPHILA SIMULANS*

Ursula E. M. Ramírez, Alejandro Sánchez-Gracia, Julio Rozas, Monserrat Aguadé

Universitat de Barcelona, Av. Diagonal 645, 08028 Barcelona, Spain

Most surveys of nucleotide variation in *Drosophila simulans*, like in *D. melanogaster*, have focused either on coding regions, or on non-coding regions adjacent to coding regions. Although mutations segregating at non-coding regions are generally considered to be neutral, their level and pattern of variation might be affected by linked selected (advantageous or deleterious) mutations in coding regions. Therefore, variation in most non-coding regions so far analyzed might be greatly affected by natural selection, even in regions of high recombination. Here, we have surveyed nucleotide variation across a 90-Kb stretch of non-coding DNA at band 98CD. The region was chosen because there was no previously annotated gene in the *D. melanogaster* genome sequence. Six ~1.5-Kb fragments at increasing distances from the two adjacent coding regions were sequenced in a sample from an African population of *D. simulans*. The level and pattern of nucleotide variation shows a non-homogeneous distribution across the region studied, which might be difficult to reconcile with both neutral and simple demographic models.

14.21P

RAPID FORMATION OF LAND RACES IN *PICEA ABIES*

[1]Tore Skrøppa, [1]Mari Mette Tollefsrud, [2]Christoph Sperisen, [1]Øystein Johnsen

[1]*Norwegian Forest Research Institute, Høgskoleveien 12, N-1432 Ås, Norway*

[2]*Swiss Federal Institute for Forest, Snow and Landscape Research, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland*

As a part of our studies on evolutionary aspects of Norway spruce Picea abies, we have examined timing of bud-set for progenies from trees planted north of native origin. Central European trees (lat. 50-52°N) have produced seeds after open pollination in stands and provenance trials located in the southeastern (lat. 60°N) and central parts (lat. 64°N) of Norway. Seedlings from these trees, the original Central European provenances, and local Norwegian provenances were grown for one season in a greenhouse. Identification of central European and northern European trees were assured by analysing the second intron of the mitochondrial nad1 gene, which is maternally inherited and uniquely discriminates between the two origins. Formation of terminal buds was recorded during late summer and autumn of 2002. Strong population differentiation along latitudinal and altitudinal gradients has repeatedly been observed in this trait, and it measures the photoperiodic sensitivity of a given plant material. Thus, bud-set is considered to reflect adaptive properties of Norway spruce. The bud-set of the seedlings from the Central European mothers was much closer to the bud-set of the local Norwegian mother trees and provenances than to that of original maternal Central European provenances. The difference is larger than could be attributed to natural selection and pollen migration from local stands. The temperature during embryogenesis in the developing seeds, which is known to affect timing of phenology and frost hardiness development in Norway spruce progeny, can additionally explain the northern performance.

14.22P

IDENTIFYING THE MECHANISTIC BASIS OF FITNESS DIFFERENCES BY CONNECTING MOLECULAR TESTS OF SELECTION WITH FITNESS MEASUREMENTS IN THE WILD

Christopher W. Wheat

Max Planck Institute of Chemical Ecology, Department of Genetics and Evolution,
Winzerlaer Strasse 10, 07745 Jena, Germany

Connecting DNA sequence variation, which rejects tests of neutral evolution, with genotypic measurements of fitness in the wild is a difficult task, given that the rejection of neutral hypotheses can be the result of non-selective factors. Moreover, even if demographic factors can be ruled out, the selection pressures that left their mark upon the gene in question may no long exist or be too weak to measure in the wild. Previous observations of fitness differences among phosphoglucose isomerase (PGI) genotypes in *Colias* butterflies indicate current overdominant balancing selection acting upon the segregating variation at this gene. Here we present a molecular analysis of the genetic variation at the PGI gene by analyzing the sequence variation within one population. By focusing on a high elevation species, *C. meadii*, which has experienced recent bottlenecks (10,000 years before present), we were able to resolve haplotypes and assess their population level frequencies. Molecular tests of selection both strongly support previous observations of balancing selection as well as identify specific regions of the PGI enzyme believed to be responsible for the overdominant biochemical differences among genotypes.

Symposium 15

Evolutionary biology of learning

Organisers: Tadeusz J. Kawecki & Sue Healy

Roger Stevens Lecture Theatre 22

09.20 – 09.50	**Braithwaite, V.** The evolutionary ecology of learning and memory
09.50 – 10.20	**Mery, F.** Fitness costs and benefits of learning: experimental evidence from *Drosophila melanogaster*
10.20 – 11.00	**Coffee**
11.00 – 11.20	**Sznajder, B.** Innate versus learned responses to prey-related cues and the evolution of learning
11.20 – 11.40	**Mallon, E. B.** Immune response inhibits memory consolidation in insects
11.40 – 12. 00	**Mappes, J.** Does natural selection favour smart birds?
12.00 – 12.20	**Jordan, W. C.** Atlantic Salmon change the expression of odorant receptor genes to learn the smell of home
12.20 – 12.40	**Ellers, J.** Testing the role of vocal learning in song divergence and male dispersal
12.40 – 14.00	**Lunch**

Invited talks

15.1

THE EVOLUTIONARY ECOLOGY OF LEARNING AND MEMORY

Victoria Braithwaite

University of Edinburgh, School of Biological Sciences, King's Buildings, Edinburgh, EH9 3JT, UK

In a variable environment animals are frequently faced with decisions, for example, which mate should I select, or, where is it safe to forage? To respond adaptively, animals compare information that is currently available with previously experienced and remembered events. In this way, learning and memory can be considered to underpin much of behavioural ecology. Recent interest in the evolutionary biology of learning has concentrated on the impact of the local environment, or ecology, and a number of studies have now revealed an important role for the local environment in shaping learning and memory abilities. The majority of these studies, however, have compared closely related species that come from different habitats. One problem with this approach is that a number of phylogenetic effects may contribute to differences in learning abilities. Using a variety of populations sampled from contrasting habitats, I have investigated the effects of different environmental variables on learning abilities within-species. In particular, I have worked on both the role of environmental stability and predation pressure. Here, I will present the results of a series of experiments that show that learning and memory abilities are fine-tuned to an animal's ecology.

15.2

FITNESS COSTS AND BENEFITS OF LEARNING: EXPERIMENTAL EVIDENCE FROM DROSOPHILA MELANOGASTER

Frederic Mery

University of Fribourg, chemin du musee 10, CH1700 Fribourg, Switzerland

The presence of genetic variation for learning ability in animals opens the way for experiments asking how and under what ecological circumstances improved learning ability should evolve. Here we report experimental evolution of learning ability in *Drosophila melanogaster*. By exposing experimental populations for more than 70 generations to conditions that we expected to favour associative learning with regard to oviposition substrate choice, we observed the evolution of both a higher learning rate and a better memory. However the evolution of the learning ability of the flies was correlated to a decrease of larval competitive ability indicating a cost of learning ability.

Contributed talks

15.3

INNATE VERSUS LEARNED RESPONSES TO PREY-RELATED CUES AND THE EVOLUTION OF LEARNING

Beata Sznajder, Martijn Egas, Iza Lesna, Maurice Sabelis

University of Amsterdam, Department of Population Biology, Kruislaan 320, 1098 SM Amsterdam, the Netherlands

The ability to learn constitutes a means of coping with changing environments. Foraging predatory mites of the species *Phytoseiulus persimilis* experience such environments. Their herbivorous prey, the generalist two-spotted spider mite, triggers the release of plant volatile compounds. The induced volatile blend is prey-specific, and thus it can serve as a cue of prey presence. Depending on the prey patch size such association of volatile blend and prey can be experienced by several generations of the predators residing in it. Ultimately some predators have to leave the overexploited patch and use volatile cues in prey search. The value of such cues however is confounded by the variation in volatile blend produced by different plant species and triggered by different herbivores. This begs the questions: how do the predators cope with the variation in prey-related cues and how does learning compare to the innate (genetic) preferences when searching for prey. We address these questions by selecting for extreme preferences in *P. persimilis* to a certain concentration of methyl salicylate (MeSa), a generally occurring component of volatile blends. Having selected lines of fixed responses we look whether there is the effect of juvenile experience on the adult preferences (imprinting) as well as the ability of adult individuals to learn to "update" the preference through the association of MeSa and prey abundance. To answer whether innate or learned preference (or avoidance) is more important we test what happens if MeSa is presented together with other volatiles associated with unfavourable food conditions. We finish by speculating on the ecological conditions leading to innate responses as well as the evolution of learning in *P. persimilis*.

15.4

IMMUNE RESPONSE INHIBITS MEMORY CONSOLIDATION IN INSECTS

[1]**Eamonn B. Mallon,** [2]Axel Brockman, [1]Paul Schmid-Hempel

[1]*ETH Zürich, ETH Zentrum, Zürich, Switzerland*

[2]*Zoologie II, Universität Würzburg, Würzburg, Germany*

In vertebrates, it is well established that there are many intricate interactions between the immune system and the nervous system and vice versa. Regarding insects, until now nothing has been known about the link between these two systems. Here we present, for the first time, behavioural evidence indicating a link between the immune system and the nervous system in insects. We show that otherwise non-infected honeybees whose immune systems are challenged by a non-pathogenic immunogenic elicitor (LPS) have reduced abilities to consolidate memories. The cost of an immune response therefore not only affects survival of the host, as previously shown, but also every-day behaviour and memory formation.

15.5

DOES NATURAL SELECTION FAVOUR SMART BIRDS?

Johanna Mappes, Rauno Alatalo, Janne Kilpimaa

University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35 40014 Jyväskylä Finland

Recently there has been vivid debate about animal cognitive abilities, asking in what extent differences in animal intelligence are results of different selection pressures. Adaptive explanation is that natural selection plays major role shaping animal cognitive abilities. To be adaptive any trait in question needs to be target of natural selection and it must have genetic basis to allow natural selection to operate. We conducted series of behavioural trials where we tested cognitive abilities of wild great tits (*Parus major*). Then we followed their winter survival. We also conducted similar tests with cross-fostered great tit juveniles to see in what extent these cognitive traits are heritable. Surprisingly we found that birds which were quick learners suffered higher predation risk compared to birds that learnt slowly. It seems that birds that are more prone to learn difficult tasks are also bolder in their overall behaviour and this may expose them to risky behaviour. We found that heritabilities of the birds' cognitive abilities were very low which may explain why individual variation in these traits is so high.

15.6

ATLANTIC SALMON CHANGE THE EXPRESSION OF ODORANT RECEPTOR GENES TO LEARN THE SMELL OF HOME

[1]**William C. Jordan**, [1]Juliet P. Dukes, [1]Robert Deaville, [2]Michael W. Bruford,
[3]Alan F. Youngson

[1]*Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK*

[2]*Cardiff School of Biosciences, Cardiff University, Cathays Park, Cardiff CF10 3TL, UK*

[3]*Fisheries Research Services, Freshwater Laboratory, Faskally, Pitlochry PH16 5LB, UK*

The ability of salmon to home to their natal stream to spawn has long intrigued biologists. It is known that olfaction is crucial to accurate homing, and that the transition between freshwater and marine environments (the parr-smolt transformation; PST) is a period of increased olfactory sensitivity and learning, resulting in a permanent memory of natal site odors that is retained in peripheral sensory neurons. These odors are then used as cues by sexually maturing fish on their homeward migration. We have used molecular techniques to demonstrate transient increases in expression of odorant receptor transcripts coincident with PST. Both olfactory and vomeronasal receptors are involved, which suggests that the fish learn both environmental odors and semiochemicals (pheromones). Receptor expression varies between families and changes over time indicating both genetic differences in odor stimuli and multiple periods of olfactory sensitivity. We hypothesise that changes in gene expression may have a role in maintaining population structure in Atlantic salmon.

15.7

TESTING THE ROLE OF VOCAL LEARNING IN SONG DIVERGENCE AND MALE DISPERSAL

J. Ellers, H. Slabbekoorn

Vrije Universiteit, Animal Ecology, De Boelelaan 1085, 1081 HV Amsterdam, Netherlands

The importance of birdsong in sexual selection and the widespread existence of geographic variation in song has raised the question whether song dialects can promote the evolution of new, reproductively isolated, subgroups. However, the effect of song learning on the relationship between song divergence and gene flow is still poorly understood. Here, we use a spatially explicit model to study the role of vocal learning mode (predispersal and postdispersal) on 1) genetic and phenotypic song divergence among populations, and 2) male dispersal among populations. The majority of scenarios simulated in the model led to significant genetic and phenotypic song divergence, consistent with the widespread occurrence of dialects in natural populations. Most importantly, song learning played a decisive role in causing an incongruence of genetic divergence and phenotypic song divergence among populations. As a consequence, song learning often prevented the expected negative relationship between the degree of song divergence and dispersal between populations, especially in postdispersal learners. These findings may help to interpret empirical data on song divergence and gene flow and provide qualitative and testable predictions for conditions under which intraspecific song variation may promote reproductive divergence and speciation.

Posters

15.8P

THE ROLE OF LEARNING IN THE ONTOGENY AND EVOLUTION OF MEGAPODES, BIRDS WITHOUT PARENTAL CARE

A. Göth, C. S. Evans

Macquarie University, Dept of Psychology, Animal Behaviour Lab, North Ryde 2109, Sydney, Australia

One of the fundamental problems in the study of behavioural development is understanding the mechanisms by which animals learn to recognise members of their own species. In most birds and mammals, early experience plays a critical role; the young animal reliably encounters at least one of its parents after hatching or birth and has the opportunity to learn about them. This process is important because it ensures short-term survival and influences mate choice decisions in adulthood. But one remarkable group of Australian birds, the megapodes, reveals that other developmental pathways can evolve: chicks do not meet their parents after hatching and thus have no opportunity to learn from them. Here we describe recent work on species recognition in chicks of the Australian brush-turkey *Alectura lathami*. Controlled experiments using taxidermically-prepared robots presented under optical filters show that socially-naive hatchlings prefer to approach conspecifics of similar colour and that short wavelengths are responsible for this effect. In addition, chicks prefer moving robots to static ones and pecking movements to a control in which the head sweeps from side to side. Morphology and behaviour hence act synergistically to account for the aggregation response. We discuss the implication of these results for the current debate concerning species recognition and speciation. In some parts of Australia, two megapode species (the brush-turkey and Orange-footed megapode *Megapodius reinwardt*) occur sympatrically and even use the same mounds of leaf litter for incubating their eggs. Chicks look similar to the human eye. It thus seems likely that there has been selection for a highly specific species recognition mechanism capable of ensuring that no 'mistakes' in mate choice are made and no interbreeding occurs. Understanding the role of experience in this process will provide insights into the relationships among learning, species recognition, mate choice and speciation.

Symposium 16

Key factors in adaptive radiation

Organisers: Konrad Bachmann & Susanne Foitzik

Conference Auditorium 1

09.20 – 09.50	**Meyer, A.** Comparative developmental and genomic approaches to the study of cichlid fish diversification
09.50 – 10.20	**Städler, T.** Genealogical footprints of speciation processes in wild tomatoes: A multilocus approach
10.20 – 11.00	**Coffee**
11.00 – 11.20	**Glaubrecht, M.** Endemic radiations in the evolutionary theatre of encient lakes: an evolutionary ecology approach exemplified by limnic gastropods in East Africa and on Sulawesi
11.20 – 11.40	**Maraun, M.** Radiation in 'ancient asexuals': oribatid mites (Acari)
11.40 – 12.00	**Mayhew, P. J.** Which clade is the greatest? Reasons why we still don't know
12.00 – 12.20	**Ruber, L.** Rapid speciation and ecological divergence in the American seven-spined gobies (Gobiidae, Gobiosomatini) inferred from a molecular phylogeny
12.20 – 12.40	**Feldhaar, H.** Is ecological speciation the driving force in the radiation of the Macaranga associated Crematogaster (Decacrema) plant-ants?
12.40 – 14.00	**Lunch**

Invited talks

16.1

COMPARATIVE DEVELOPMENTAL AND GENOMIC APPROACHES TO THE STUDY OF CICHLID FISH DIVERSIFICATION

Axel Meyer

Department of Biology, University of Konstanz, Universitätsstr. 10, D-78457 Konstanz, Germany

The large lakes in East Africa each contain a species flock composed of hundreds of species of cichlid fishes. The adaptive radiations of cichlid fishes are characterized by their extremely fast rates of speciation and their high diversity in terms of species. We are using comparative developmental and genomic approaches to gain a better understanding of the developmental and molecular basis for their diversification. I will report on work from my lab on comparative analyses of Hox cluster evolution in cichlids compared to other fishes and tetrapods where we find that fishes have a particularly high rate of evolution and that there is a surprisingly large amount of variation in the architecture of Hox clusters. Results from studies on candidate genes for colorational diversification in cichlids show that there maybe rather simple differences in RNA-splicing that can result in pronounced colorational differences. Such differences in coloration may, through mechanisms of sexual selection, result in speciation.

16.2

GENEALOGICAL FOOTPRINTS OF SPECIATION PROCESSES IN WILD TOMATOES: A MULTILOCUS APPROACH

Thomas Städler, Kerstin Roselius, Wolfgang Stephan,

University of Munich (LMU), Dept. Biologie II, Luisenstrasse 14, 80333 Munich, Germany

Wild relatives of the cultivated tomato (genus *Lycopersicon*) exhibit a considerable diversity of mating systems, encompassing both highly selfing and obligately outcrossing taxa. While these tomato species are quite distinct morphologically, molecular evidence is mounting that they may be products of a fairly recent radiation. Here, we report on our ongoing project which utilizes multilocus nuclear gene sequences in a genealogical framework. From a technical point of view, such an approach is facilitated due to the availability of excellent genetic maps and known recombination rates across the genome. We assess levels of DNA sequence variation and haplotype structure at multiple loci across the genome in five tomato species. To exploit genealogical information contained in the sequence data, we apply the "isolation" model of Wakeley & Hey (1997). This coalescent-based model assumes that an ancestral species split into two descendent, allopathic species, with no further gene flow between the incipient taxa. The genealogical information represented by various classes of segregating sites (i.e. shared polymorphisms, sites polymorphic in only one of two taxa, and fixed differences between species) is extracted to yield estimates of the model parameters, including the scaled divergence time between species. We hope to eventually gain insights into demographic aspects of speciation processes, including information about relative magnitudes of effective population size. The multilocus sequence data also allow us to jointly analyze effects of the mating system and various forms of selection on levels and patterns of molecular variation and divergence. Of particular interest is the role of the mating system and its potential co-variation with demographic factors, such as events of local extinction and recolonization. In the future, it will be of paramount importance to extend all analyses to multiple populations per species.

Contributed talks

16.3

ENDEMIC RADIATIONS IN THE EVOLUTIONARY THEATRE OF ENCIENT LAKES: AN EVOLUTIONARY ECOLOGY APPROACH EXEMPLIFIED BY LIMNIC GASTROPODS IN EAST AFRICA AND ON SULAWESI

Matthias Glaubrecht

Institute of Systematic Zoology, Museum fuer Naturkunde, Invalidenstr. 43, 10115 Berlin, Germany

Speciation and the origin of radiations on oceanic as well as in lacustrine islands have featured prominently among the discussions in evolutionary biology, viewing these isolated ”evolutionary theatres” as hotspots of diversification. While vertebrates such as finches or cichlids have been studied intensively, providing instructive examples of rapid radiations, other organisms often exhibiting even more dramatic levels of endemisms only recently became the subject of interest. Using limnic gastropods as model system here, the role of extrinsic and intrinsic factors is investigated for the presumptive endemic evolution of so-called "thiarid" species flocks in East African Lake Tanganyika and the central lakes on Sulawesi (i.e. Lake Poso and the lakes of the Malili system, e.g. Matano, Mahalona, and Towuti).

Based on a revised cerithioidean phylogeny that identifies five limnic families as separate clades (i.e. Melanopsidae, Pleuroceridae, Pachychilidae, Thiaridae s. str. and Paludomidae), and in analysing morphological and molecular data on various hierarchical levels (from families to populations), the two different model systems in Africa and on Sulawesi are compared within the framework of an evolutionary ecology approach, understood here as aiming to reconstruct the origin and alteration of the ecological interrelations of organisms and their respective environments in the course of evolution. This approach provides a research program for acquiring a synthetical perspective, including morphology, molecular genetics, ecology and biogeography. It will be shown (i) why and how earlier attempts to evaluate responsible factors in the radiations were essentially suffering from lacking insight into the systematics and morphology (in partiular reproductive biology) of limnic gastropods, and (ii) that differences in the geological setting are crucial (e.g. rifting in c. 12 myr old Lake Tanganyika vs. Sulawesi's composite terrane origin with c. 1-2 myr old lakes). A synthetic scenario is outlined incorporating historical and ecological aspects as well as important biological features such as viviparity and trophic specializations.

16.4

RADIATION IN 'ANCIENT ASEXUALS': ORIBATID MITES (ACARI)

[1]**M. Maraun**, [1]M. Heethoff, [1]K. Schneider, [1]S. Scheu, [2]R.H. Thomas, [3]R.A. Norton,

[1]*TU Darmstadt, Institut fuer Zoologie, Schnittspahnstrasse 3, 64287 Darmstadt, Germany*

[2]*Natural History Museum London, Dep. of Zoology, Cromwell Road, SW7 5BD, London, UK*

[3]*State University of New York, College of Environmental Science and Forestry, Faculty of Environmental and Forest Biology, 1 Forestry Drive, Syreacuse NY 13210, USA*

Nucleotide sequences of the D3 expansion segment and its flanking regions of the 28S rDNA gene were used to evaluate phylogenetic relationships among representative sexual and asexual oribatid mites (Oribatida, Acariformes). The aim of this study was to investigate the hypothesis that oribatid mites consist of species rich clusters of asexuals that radiated while being parthenogenetic. Furthermore, the phylogenetic position of the astigmate mites (Astigmata, Acariformes) is investigated. It has been hypothesised that Astigmata represent a paedomorphic and sexually reproducing lineage within a cluster of parthenogenetic oribatid mites (Malaconothroidea) indicating the re-evolution of sex and a subsequent radiation.

We present the first phylogenetic tree of oribatid mites s.l. (incl. Astigmata) based on nucleotide sequences. Intraspecific genetic variation in the D3 region was low suggesting that this region can be used as a species marker. Results from the neighbour joining (NJ) and maximum parsimony (MP) algorithms indicate that species rich parthenogenetic groups including Camisiidae, Nanhermanniidae and Northridae are monophyletic, consistent with the hypothesis that some oribatid mites, as proposed earlier. However, the proposed relationship with Malaconothroidea was not supported. Results of this study indicate that parthenogenesis is not a dead end in evolution; in oribatid mites multiple ancient asexual clusters evolved independent of each other.

16.5

WHICH CLADE IS THE GREATEST? REASONS WHY WE STILL DON'T KNOW

Peter J. Mayhew

University of York, Department of Biology, PO Box 373, York YO10 5YW, UK

I investigate which event in hexapod evolution has done most to fill up the world with species, using state-of-the-art methodology and data. The question demands that we a) identify significant shifts in diversification rate and b) can estimate their effects on current species richness. Nested sister taxon comparisons suggest that the Neoptera, Coleoptera and Diptera are significant radiations. Parsimony analysis, although agreeing about the importance of the Coleoptera and Diptera, and of the unimportance of the Insecta, suggests that the most even when nested within a large phylogeny, may seriously misrepresent events at their base. I conclude that not only are the necessary data not adequate to answer the question, neither too are the statistical methods. I outline a method that might provide a more satisfactory solution.

16.6

RAPID SPECIATION AND ECOLOGICAL DIVERGENCE IN THE AMERICAN SEVEN-SPINED GOBIES (GOBIIDAE, GOBIOSOMATINI) INFERRED FROM A MOLECULAR PHYLOGENY

[1]**Lukas Ruber**, [2]James L. Van Tassell, [3]Rafael Zardoya,

[1]*Museo Nacional de Ciencias Naturales, Jose Gutierrez Abascal 2, 28006 Madrid, Spain*
[2]*Hofstra University, Hempstead, NY 11549, USA*
[3]*Museo Nacional de Ciencias Naturales, Jose Gutierrez Abascal 2, 28006 Madrid, Spain*

The branching pattern of a phylogenetic tree can be used to detect changes in speciation rate through time, and to detect asymmetries between contemporaneous clades in their number of descendant species. Such information is needed to distinguish speciation bursts from stochastic background rates and may help to identify adaptive radiations and key innovations underlying the emergence of rapid ecological and phenotypic divergence within a lineage. The American seven-spined gobies (Gobiidae: Gobiosomatini) represent a possible case of a marine adaptive radiation. With over 130 species in 24 genera the Gobiosomatini is a highly diverse group of marine fishes endemic to the New World, with many endemics in the Caribbean region, that exhibits astonishing morphological, behavioural, and ecological adaptations. We have reconstructed a molecular phylogeny of 54 Gobiosomatini taxa (65 individuals) based on a 1,646-bp region that includes the mitochondrial 12S rRNA, tRNA-Val, and 16S rRNA genes. We use the molecular phylogeny to study the dynamics of speciation in the Gobiosomatini by testing for departures from the constant speciation rate model. We observe a burst of speciation in the early evolutionary history of the group. Our results further show a split among the main clades into coastal-estuarine, deep-ocean, and tropical reef habitats. These major habitat shifts account for the early significant acceleration in lineage splitting and the initial divergence of the main Gobiosomatini clades. Subsequent diversification is found to be triggered by behaviour and niche specialisations at least in the reef associated clades. Our results indicate that the diversity of the Gobiosomatini has arisen during episodes of adaptive radiation and emphasise the importance of ecology in marine speciation.

16.7

IS ECOLOGICAL SPECIATION THE DRIVING FORCE IN THE RADIATION OF THE *MACARANGA* ASSOCIATED *CREMATOGASTER* (DECACREMA) PLANT-ANTS?

[1]**Heike Feldhaar**, [2]Brigitte Fiala, [1]Jürgen Gadau,

[1]*Zoologie II, Biozentrum der Universität Würzburg, Am Hubland, 97074 Würzburg, Germany*

[2]*Zoologie III, Biozentrum der Universität Würzburg, Am Hubland, 97074 Würzburg, Germany*

In one of the most species-rich ant-plant symbiotic systems worldwide pioneer trees of the genus *Macaranga* (Euphorbiaceae) are inhabited by specific partner ants, mostly of the genus *Crematogaster* (subgenus Decacrema). Both mutualistic partner groups show considerable radiation and in spite of the frequently sympatric occurrence of several host-plant species reoccurring and non-random association patterns are observed.

Such obligate ant-plant associations have long been viewed as classical examples of strict coevolution. However, the comparison of the phylogenies of Decacrema-morphospecies (mtDNA) (Feldhaar et al. 2003, Mol. Phylogenet. Evol., in press) with that of their Macaranga-host plants (ITS) (Blattner et al. 2001, Mol. Phylogenet. Evol. 19: 331-334) does not suggest strict cocladogenesis between the two species groups. Our results rather support the view that host-shifting or host-expansion is common in the ants colonizing *Macaranga*. Conflicting results between phylogenies derived from mtDNA and nuclear genes of these ants point towards hybridization between at least two morphologically and ecologically distinct morphospecies inhabiting the same host–plant species. Such rare hybridization events could lead to the introgression of adaptive traits, thus possibly facilitating host-shifts.

We consider ecological speciation a likely mechanism of speciation for the *Macaranga*-associated *Decacrema* ants. Differences in *Macaranga* host-plants (which may be seen as the biotic environment of the partner-ants) would then result in functional and phenotypic differentiation in the ants due to divergent selection. First results from field studies show that different but closely related *Decacrema* species colonizing the same *Macaranga* species show differences in traits associated with host usage. We therefore compared worker density of colonies, pruning behaviour and levels of aggression of two morphospecies inhabiting the same host plant species.

Posters

16.8P

MECHANISMS OF SPECIATION IN SYMPATRY IN THE POLYMORPHIC NEOTROPICAL MIDAS CICHLID COMPLEX

Marta Barluenga, Axel Meyer

University of Konstanz, Universitaetsstr.10, 78457 Konstanz, Germany

Recently, both theoretical and empirical evidence for sympatric speciation suggested that under some conditions speciation in sympatry is possible. The Midas Cichlid species complex (*Amphilophus* spp.) from several crater lakes in Nicaragua fits several of the key characteristics of these model with strong assortative mating on the basis of a color polymorphism coupled with trophic and ecological differentiation based on morphological traits as body shape or trophic apparatus. We used microsatellite markers and sequences of the mtDNA control region to study the population genetic structure of Midas Cichlid populations from the two Great Lakes and three crater lakes in Nicaragua, Central America. We found both allopatric differentiation of geographically isolated populations and sympatric differentiation of coexisting populations. Ecological specialization to local environments appears to be the main force of speciation in the Midas Cichlid complex, but sexual selection also contributes to the differentiation of populations in sympatry. The evolution of the Midas Cichlid species complex in Nicaragua follows common patterns of cichlid evolution in lacustrine environments, and appears to be an excellent model for the study of early stages of adaptation and speciation of East African cichlid lacustrine flocks.

16.9P

AGE AND DIVERSITY OF SOCIAL PARASITES IN THE ANT TRIBE FORMICOXENINI

Jeanette Beibl, Susanne Foitzik, Jürgen Heinze

Lehrstuhl Biologie I, Universität Regensburg, Universitätsstr. 31, 93040 Regensburg, Germany

Social parasitism, i.e., the temporary or permanent parasitic dependence of one species of social insects on another, is particularly common in the ant tribe Formicoxenini. although this taxon represents less than 3 % of the approximately 11000 described ant species, it contains more than 10 % of the 300 known parasitic ants. Furthermore, social parasitism - slave-making and workerless inquilinism – has evolved convergently several times within the Formicoxenini, with the different lineages showing different degrees of diversity. Until now it is unclear, which factors favour the evolution of parasitic founding and the diversification of social parasites. In this study we investigate the genetic diversity within the five slave-making monophyla *Protomognathus americanus*, *Leptothorax duloticus*, *Harpagoxenus* (three species), *Chalepoxenus* (five or more species) and Epimyrma (more than eight species), and the workerless inquiline *Leptothorax minutissimus* to determine the age of the different taxa. In addition, we studied several *Leptothorax* hosts species that are parasitised by these taxa. We sequenced more than 600bp of the mitochondrial Cytochrome Oxidase gene from live or alcohol material of nearly 40 parasites: the relatively old genera *Harpagoxenus, Protomognathus, Epimyrma*, and *Chalepoxenus,* and two young taxa that evolved from their *Leptothorax* hosts only recently the slave-maker *Leptothorax duloticus* and the inquiline *Leptothorax minutissimus*. Thus, age alone can not explain the difference in species numbers between the different parasitic taxa. Supported by the DFG (He 1623/13-1).

16.10P

DOES POLLEN FEEDING HAVE A SINGLE ORIGIN IN *HELICONIUS* BUTTERFLIES?

Margarita Beltran

University College London, 4 Stephenson Way, London NW1 2HE

The genus *Heliconius* or passion-vine butterflies and its relatives *Laparus, Eueides* and *Neruda* are one of the best known groups of neotropical butterflies. These four genera have undergone rapid speciation and divergence. Additionally, this genus has been considered one of the most remarkable examples of mimicry, and it has been important in understanding ecological processes like coevolution between insects and plants. A well resolved phylogenetic hypothesis for the group is needed to understand how unique traits such as pollen feeding evolved, and to test the role of mimicry in driving speciation. A recent morphogical study suggested that adult pollen feeding has evolved twice, in the genera *Laparus* and *Heliconius*, but mtDNA sequence data places the species *Laparus doris*, and the genus *Neruda*, within *Heliconius*, suggesting a single origin of pollen feeding. Here I address the question: Is *Heliconius* a monophyletic lineage? I sampled 111 individual butterflies, representing 37 *Heliconius*, 1 *Laparus*, 2 *Neruda*, 10 *Eueides*, and 10 outgroup species and sequenced COI and COII mtDNA and a nuclear marker Elongation factor 1µ. Additionally, representative individuals from each genus were sequenced for 16s mtDNA and two further nuclear genes *Apterous* and *Decapentaplegic* making a total of 2100bp of mtDNA and 1245bp of nuclear sequence. The results suggested that *Heliconius* is paraphyletic, with *Laparus doris* falling within the genus, demonstrating a single origin for pollen feeding. However different genes do not produce a clear agreement as regards relationships of the genera *Neruda* and *Laparus* within *Heliconius*, suggesting a rapid basal radiation of *Heliconius*.

16.11P

GENETIC DIFFERENTIATION IN PLANT INVASIONS: A CASE STUDY ON GARLIC MUSTARD (*ALLIARIA PETIOLATA*)

[1]Oliver Bossdorf, [1]Daniel Prati, [2]Bernhard Schmid, [1]Harald Auge

[1]*UFZ Centre for Environmental Research, Department of Community Ecology, Theodor-Lieser-Str. 4, D-06120 Halle, Germany*

[2]*Institut für Umweltwissenschaften, Universität Zürich, Winterthurerstr. 190, CH-8057 Zürich, Switzerland*

Invasive species are confronted with environments that are characterized by many novel selection pressures, in particular biotic interactions. Therefore biological invasions provide unique opportunities for studying fundamental ecological and evolutionary processes. A particularly intriguing question is whether rapid adaptation plays a role in the success of invaders. While molecular markers can detect origin and pathways of an invasion, only comparative experiments can demonstrate differentiation in ecologically relevant traits. One way to address this issue in plants is to compare the offspring from several native and introduced populations in a common environment. We have carried out a series of such studies with garlic mustard (Alliaria petiolata) as a model system. Among others, we have used palatability tests, clipping and insect exclosure experiments to investigate whether plant defense has evolved in response to the novel, at least partly enemy-free, conditions. Other experiments adressed the competitive abilities, allelopathic potential, and plasticity to shading of native European versus introduced US populations. We will present the results of these studies and discuss their joint ecological and evolutionary implications.

16.12P

EVOLUTIONARY DYNAMICS OF HOST PLANT USE IN GALL WASPS: PHYLOGENETIC INFERENCES

A. Hernandez, J. M. Cook

Department of biological sciences, Imperial college, Silwood park, Buckhurst road, Ascot, Berkshire, Sl5 7PY

Oak gall wasps (Hymenoptera: *Cynipidae, Cynipini*) are characterized by their alternating parthenogenetic and sexual generations and by their ability to induce a wide diversity of highly complex species- and generation-specific galls on oak trees. In European members of the Cynipini family each generation is specific to either the white oak or the black oak Quercus section. In addition the different generations of a single species may be both on white oaks, both on black oaks, or one on each. This life cycle diversity is evident mostly between genera, but also within one large genus Andricus. Prior to this study the phylogenetic relationships of the different oak gallwasp genera were poorly resolved, preventing accurate inference of the evolution of host use. I first assessed the utility of three DNA sequence markers (long- wavelength opsin, 28s rDNA and cytochrome b) in reconstructing phylogenetic relationships within and between genera of European Cynipini. I report sequence divergence values, saturation levels and compare phylogenetic results of the sequences analysed both separately and combined. The data indicate that 28s and opsin are most informative between genera, while Cyt b shows great A-T bias, high levels of saturation and significant conflict in phylogenetic signal when compared with the other two genes. I therefore used the 28s + opsin phylogeny to analyse host oak use at the genus level, showing that there have been multiple independent host shifts from white to black oaks. In addition, the evolution of host oak use in the sexual and asexual generations appears to be linked. These changes in life cycle demonstrated have considerable impact upon the population biology of the species involved and also open up new niches for species radiations.

16.13P

RAPID EVOLUTION OF PREMATING REPRODUCTIVE ISOLATION IN ACOUSTICALLY COMMUNICATING GRASSHOPPERS

Frieder Mayer, Brigitte Gottsberger, Otto von Helversen

University of Erlangen, Institute of Zoology II, Staudtstrasse 5, D-91058 Erlangen, Germany

The analysis of mechanisms how populations differentiate and new species arise, is fundamental for understanding the evolution of biological diversity. Mating preferences and sexually selected characters can rapidly diverge between populations, and this probably can lead to premating reproductive isolation and hence the evolution of new species. We investigated the role of a bidirectional acoustic communication system for the radiation of grasshoppers (Acrididae, Orthoptera). Most species of the subfamily Gomphocerinae produce species-specific songs, which allow the recognition, localisation and selection of conspecific mating partners. DNA sequences were used to estimate divergence times of closely related species, which produce complex calling songs. Species with rather similar morphology but highly divergent calling songs were genetically very similar. They even could share identical DNA sequences of a 600 bp fragment of the mitochondrial CO1 gene. This indicates that the coevolution of male song characters and female preferences of acoustic signals evolved rapidly and led to premating reproductive isolation.

16.14P

SPECIATION IN ASEXUAL POPULATIONS IN SYMPATRY AND PARAPATRY

[1]Jitka Polechova, [2]N. H. Barton

[1]*Charles University, Prague, Vinicna 7, 126 80 Praha 2, Czech Republic*

[2]*ICAPB, University of Edinburgh, W. Mains Rd., EH9 3JT Edinburgh, Scotland*

While biogeographic evidence and theory have led to the view that allopatric divergence predominates, recent theory has relaxed the constraints on sympatric and parapatric speciation. Dieckmann and Doebeli (1999) claim a rather high probability of sympatric speciation in single populations with unimodal carrying capacity, for both asexually and sexually reproducing populations. In a subsequent model (2003) these authors argue that clumping due to frequency-dependent competition is even more likely in spatially structured populations along an environmental gradient We concentrate on the asexual model and assess possible causes of clumping to discrete phenotypes. Specifically, we argue that in sympatric populations with frequency-dependent competition as modelled in DD (1999) two discrete phenotypes can be stable for a reasonably long time only under rather limited conditions. Conversely, the unimodal equilibrium predicted by Roughgarden (1972) will be filled by more phenotypes, so that there is negligible disruptive selection necessary for reinforcement. Here, we show that in DD's (2003) model, parapatric clumping emerges naturally when the spatial range is limited, as a result of reduced maladaptive geneflow at the edges. We also analyse the importance of this phenomenon for phenotypic clumping in asexual populations, and assess the importance of random drift and other irregularities in the system.

16.15P

A MULTILOCUS APPROACH TO SPECIATION IN *LYCOPERSICON*: GENETIC DIVERSITY AND RECOMBINATION IN SPECIES OF WILD TOMATOES

K. Roselius, G. Feldmaier-Fuchs, T. Städler, W. Stephan

Ludwig-Maximilians-University Munich, Luisenstr. 14, 80333 Munich, Germany

We investigate effects and interactions between mating system, genomic recombination rate, demography, and natural selection on genetic diversity within and between five species of the genus *Lycopersicon* (wild tomatoes). The species in our study are morphologically distinct and show a range of mating systems from obligate outcrossing (self-incompatible) to highly selfing (self-compatible). Molecular data suggest a recent divergence, which makes this radiation an ideal model system to study processes of speciation with population-genetic methods. DNA sequence variation is measured by using single-nucleotide polymorphisms, indels, and microsatellites in multiple, single-copy nuclear genes. Silent molecular variation is compared to various estimates of recombination: the population recombination rate was estimated with Hudson's (1987) method and the program LDhat (McVean et al. 2002) which uses the approximate-likelihood coalescent method of Hudson (2001). Additionally, recombination rates for each locus are estimated from a quantitative cytogenetic map based on recombination nodules (Stephan and Langley 1998). In maize the interplay between mutation, selection and recombination generates varying patterns of correlation between different measures of recombination and genetic variation (Tenaillon et al. 2002). In wild tomatoes the mating system seems to have a crucial impact on levels of within-population nucleotide variation; the self-compatible species show much lower silent variation than the self-incompatible species (Baudry et al. 2001; our new results). Together with apparently weak effects of recombination on levels of neutral variation, this suggests that population subdivision and demographic factors are important determinants of local genetic diversity.

16.16P

HOW DO TRADE-OFFS INFLUENCE THE EVOLUTION OF RESOURCE POLYMORPHISMS?

[1]C. Rueffler, [2]Tom J. M. Dooren

[1]*Theoretical Biology, Institute of Biology, Leiden University, Kaiserstraat 63, 2311 GP Leiden, The Netherlands*

[2]*Animal Ecology, Institute of Biology, Leiden University, Kaiserstraat 63, 2311 GP Leiden, The Netherlands*

Adaptive radiation often corresponds to a splitting of taxa where each new type starts specializing on a different resource. In general, an organism well adapted to one resource will be less efficient in utilizing others. We present a model with two different resources and explore under which conditions a monomorphic population might evolve into a dimorphic population. We model the evolutionary process by using the adaptive dynamics framework. Trade-offs appear to be a key factor in adaptive radiation. The shape of the trade-off decides which scenario out of three possible ones takes place: (1) Directional selection leads towards an evolutionarily stable intermediate strategy using both resources (generalist, no adaptive radiation). (2) Directional selection leads towards a population of generalists, which then experience disruptive selection. In this case the population becomes dimorphic and adaptive radiation takes place. (3) The generalist strategy is evolutionarily repelling. Evolution leads towards one specialist and one resource is not used. The population can only become dimorphic by immigration of the other specialist. Trade-off curves determined from foraging efficiency experiments in crossbills and threespine sticklebacks are in accordance with the pattern that leads to scenario (2), hence adaptive radiation in those systems can be understood by our model.

16.17P

EVOLUTIONARY GENOMICS - THE EST SEQUENCING OF AN EAST AFRICAN CICHLID

Walter Salzburger, Dirk Steinke, Axel Meyer

Department of Biology, University Konstanz, Universitaetsstrasse 10, 78457 Konstanz, Germany

The adaptive radiations of cichlid fishes in the East African Great Lakes remain the most astounding examples of morphologically, behaviourally and ecologically diverse species flocks. The intriguing diversity and species richness of the species flocks of lakes Tanganyika, Malawi and Victoria, each of which comprising hundreds of endemic species, upraised them to a prime model system for the study of evolution. One of the most outstanding facets of cichlids evolution is that the diversification of species has occurred at an unprecedented speed, and for a long time researchers focused on the question: Why are there so many cichlid species? We use a genomic approach including the sequencing of 30.000 expressed sequence tags (ESTs) of an East African cichlid species in order to investigate the key factors for the evolutionary success of the cichlids on the genomic level.

Symposium 17

The evolutionary biology of complex phenotypes

Organisers: Massimo Pigliucci & Katherine Preston

Conference Auditorium 2

09.20 – 09.50	**Preston, K. A.** Phenotypic integration: the challenges of studying the evolution of complex phenotypes
09.50 – 10.20	**Klingenberg, C. P.** Integration in complex morphological structures: from developmental processes to evolutionary potential
10.20 – 11.00	**Coffee**
11.00 – 11.20	**Astles, P.** Potential for character state evolution in response to an indirect ecological effect
11.20 – 11.40	**Hermisson, J.** The evolution of the genetic architecture of complex traits under selection and constraint
11.40 – 12.00	**Townsend, J. P.** Population Genetic Variation in Genome-wide Gene Expression
12.00 – 12.20	**Forsman, A.** Correlated evolution of conspicuous coloration and body size in poison frogs (Dendrobatidae)
12.20 – 12.40	**Davidowitz, G.** The physiological regulation of insect body size
12.40 – 14.00	**Lunch**

Invited Speakers

17.1

PHENOTYPIC INTEGRATION: THE CHALLENGES OF STUDYING THE EVOLUTION OF COMPLEX PHENOTYPES

[1]Massimo Pigliucci, [2]**Katherine A. Preston**

[1]*University of Tennessee, Depts of Botany and of Ecology and Evolutionary Biology, Knoxville TN, USA*

[2]*Stanford University, 351 Serra Mall, Stanford CA, USA*

Studies of phenotypic integration address complex patterns of covariation among the numerous interrelated characters that make up a functioning organism. Work in a variety of fields has asked the basic question of how these trait relationships evolve and what processes affect their evolution. Some of the more well-explored facets of the problem include genetic and developmental constraints on multivariate evolution, the potential for phenotypic plasticity in suites of traits, and macroevolutionary patterns in trait relationships. Recent interest in phenotypic modularity and the definition of characters has helped to firm up the concept of phenotypic integration, and advances in comparative biology and evolutionary genetics have opened the way to increasingly robust analyses of multivariate evolutionary patterns. Yet the problem of evolution in integrated phenotypes brings into focus several outstanding challenges in biology, including the need to understand the interplay between adaptation and constraint, and the difficulties of identifying appropriate statistical and conceptual models for inferring complex processes. The intrinsically interdisciplinary nature of this work is both a challenge to this growing field and one of its strengths. The authors in this symposium will present aspects of an ongoing synthesis in the field.

17.2

INTEGRATION IN COMPLEX MORPHOLOGICAL STRUCTURES: FROM DEVELOPMENTAL PROCESSES TO EVOLUTIONARY POTENTIAL

Christian Peter Klingenberg

School of Biological Sciences, University of Manchester, 3.614 Stopford Building, Oxford Road, Manchester M13 9PT, United Kingdom

Morphological characters are integrated into complexes of traits that are developmentally related, often called modules. Such integration into modules arises through interactions of the developmental pathways that produce the traits in question and manifests itself as covariation of traits in the resulting morphological structures. Analyses of the covariation of traits in morphometric data, and particularly the covariation of left-right asymmetries among traits, can be used to infer the developmental relationships and delimit modules. In addition to direct interactions among developmental pathways, there are also other mechanisms that contribute to covariation among traits, for instance, environmental factors that influence multiple traits simultaneously or allelic variation in genes that affect several traits. The origin of covariation also is likely to have effects on the long-term evolution of genetic variability. Direct interactions of developmental pathways can influence the phenotypic effects of many genes simultaneously, and the patterns of integration of those gene effects will evolve through changes of the interactions of pathways, which may be subject to substantial constraints. In contrast, integration by simultaneous effects of single genes on several traits may be evolutionarily more flexible because their effects on each trait may be controlled by distinct units of gene regulation, which can evolve separately.

Contributed talks

17.3

POTENTIAL FOR CHARACTER STATE EVOLUTION IN RESPONSE TO AN INDIRECT ECOLOGICAL EFFECT

Philip Astles, Richard Preziosi

University of Manchester, Oxford Rd, Manchester, UK

When one species interacts directly with two other species it may facilitate an interaction between these other species that would not occur in its absence. Such Indirect Ecological Effects (IEEs) have been shown to be widespread and often as strong as direct interactions in field communities. For evolution to occur in response to these IEEs the affected traits must have a genetic basis. Systems consisting of species on three trophic levels (tri-trophic), provide an opportunity to investigate the genetics of response to IEEs. We are using a tri-trophic system to investigate the IEE of two species of aphid host plant on an aphid predator, the ladybird beetle *Harmonia axyridis*, through a clone of the pea aphid *Acyrthosiphon pisum*. Aphids were collected from plants, frozen and fed to ladybird beetles in the laboratory. In this way the effect of aphid host plant could be investigated without the ladybirds ever directly encountering the plant itself. We used a full-sib, split-family experimental design to estimate genotype-by-indirect environment (G x Ei) interactions, between-environment genetic correlations, and heritabilities for a number of ladybird morphological and life history characters. Significant G x Ei and genetic correlations of less than one for some ladybird traits indicates the presence of genetic variation for response to the host plant of their prey. If part of this genetic variation is additive these ladybird traits have the potential to evolve in response to selection caused indirectly by the host plant of their aphid prey.

17.4

THE EVOLUTION OF THE GENETIC ARCHITECTURE OF COMPLEX TRAITS UNDER SELECTION AND CONSTRAINT

[1]**Joachim Hermisson**, [2]Thomas F. Hansen, [3]Gunter P. Wagner

[1]*Dept. Biology II, Ludwig-Maximilians University Munich, Luisenstr. 14, 80333 Munich, Germany*

[2]*Dept. of Biol. Sci., Florida State University, Tallahassee, FL 32306, USA*

[3]*EEB Dept., Yale University, New Haven, CT 06520-8106, USA*

We investigate how the genetic architecture of a complex (epistatic) trait is shaped under the combined action of natural selection and variational constraints. From analytical results in multilocus-models, we predict measurable patterns in the mutational effect distribution that emerge in mutation-selection equilibrium.

Implications are drawn on the evolution of genetic robustness (canalization) and on a potential "positive role" (S.J. Gould) of constraints for the continuing evolutionary process.

17.5

POPULATION GENETIC VARIATION IN GENOME-WIDE GENE EXPRESSION

[1]**Jeffrey P. Townsend,** [2]Duccio Cavalieri, [3]Daniel L. Hartl

[1]*University of California, 111 Koshland Hall, Berkeley, CA 94720 USA*

[2]*Harvard University, 7 Divinity Avenue, Cambridge, MA 02138 USA*

[3]*Harvard University, 16 Divinity Avenue, Cambridge, MA 02138 USA*

Evolutionary biologists seek to understand which traits display variation, are heritable, and influence differential reproduction, because such traits respond to natural selection and underlie organic evolution. Selection acts upon individual differences within a population. Whether individual differences within a natural population include variation in gene expression levels has not yet been addressed on a genome-wide scale. Here we use DNA microarray technology for measuring comparative gene expression and a refined statistical analysis for the purpose of comparing gene expression levels in natural isolates of the wine yeast *Saccharomyces cerevisiae*. A method for the Bayesian analysis of gene expression levels is used to compare four natural isolates of *S. cerevisiae* from Montalcino, Italy. Widespread variation in amino acid metabolism, sulfur assimilation and processing, and protein degradation - primarily consisting of differences in expression level smaller than a factor of two - is demonstrated. Genetic variation in gene expression among isolates from a natural population is present on a genomic scale. It remains to be determined what role differential gene expression may play in adaptation to new or changing environments.

17.6

CORRELATED EVOLUTION OF CONSPICUOUS COLORATION AND BODY SIZE IN POISON FROGS (DENDROBATIDAE)

Anders Forsman, Mattias Hagman

University of Kalmar, Department of Biology and Environmental Sciences, SE 391 82 Kalmar, Sweden

Conspicuous coloration is often used in combination with chemical defenses to deter predators from attacking. Experimental studies have shown that the avoidance inducing effect of conspicuous prey coloration increases with increasing size of pattern elements and with increasing body size. Here we use a comparative approach to test the prediction from these findings, namely that conspicuous coloration will evolve in tandem with body size. In our analysis, we use a previously published mitochondrial DNA-based phylogeny and comparative analysis of independent contrasts to examine if evolutionary shifts in color pattern have been associated with evolutionary changes in body size in aposematic poison frogs (Anura: Dendrobatidae). Information on body size (snout to vent length) and coloration were obtained from the literature. Two different measures of conspicuousness, in terms of contrast to leaf-littered background, were used, one based on rankings by human observers and the other based on computer analysis of digitized photographs. The results from comparative analyses using either measure of coloration indicated that avoidance inducing coloration and body size have evolved in concert in poison frogs. Results from reconstruction of character change further indicate that the correlated evolution of size and coloration has involved changes in both directions within each of the different clades of the phylogenetic tree. This finding is consistent with the hypothesis that selection imposed by visually guided predators has promoted phenotypic and genetic integration of size and coloration either by enhancing the evolution of larger body size in species with conspicuous coloration, or by enhancing evolution of conspicuous coloration in larger species.

17.7

THE PHYSIOLOGICAL REGULATION OF INSECT BODY SIZE

[1]**Goggy Davidowitz**, [2]H. Frederik Nijhout, [2]Louis J. D'Amico, [3]Derek A. Roff

[1]*University of Arizona, Dept. of Ecology and Evolutionary Biology, BSW 310, Tucson, AZ 85721 USA*

[2]*Duke University, Dept. of Biology, Durham, NC 27708 USA*

[3]*University of California, Riverside, Dept. of Biology, Riverside, CA 92521 USA*

Remarkably little is known about the developmental and physiological mechanisms that determine body size, or about the mechanisms by which an organism translates different environmental signals that result in plasticity of body size. We propose a model for body size regulation in the holometabolous tobacco hornworm (*Manduca sexta*: Sphingidae). We demonstrate that adult body size is regulated by three factors: growth rate, the timing of juvenile hormone decay as measured by the critical weight, and the timing of secretion of prothoracicotropic hormone (PTTH) and ecdysteroids, as measured by the PTTH delay time. We show that differential sensitivity of these three factors to temperature versus diet quality is the primary mechanism enabling differential plasticity responses of body size to different environmental stimuli. Body size increased at lower temperatures and on higher quality diets, critical weight was higher on higher quality diets but did not change with temperature, PTTH delay time increased at lower temperatures but did not change with diet, and growth rate increased at higher temperatures and on higher quality diets. Therefore, plasticity of size in response to diet quality is regulated primarily by changes in growth rate and critical weight, while plasticity of size in response to temperature is regulated primarily by changes in PTTH delay time and growth rate. Analyses of genetic variances and covariances indicate that while there was genetic variation for plasticity of size and plasticity of growth rate, there was no genetic variation for the plasticities of critical weight and PTTH delay time, suggesting that while these latter two factors may enable the evolution of body size, they may also constrain the evolution of plasticity of size. Thus, the mechanism regulating body size differs from the mechanism regulating plasticity of size. This study provides the first evidence for how each of the main components of variance of a trait may be independently regulated.

Posters

17.8P

GENOMIC ANALYSIS OF PHENOTYPIC PLASTICITY IN NEOLAMPROLOGUS BRICHARDI, A COOPERATIVELY BREEDING CICHLID FISH.

[1]Nadia Aubin-Horth, [1]Seth A. Ament, [2]Sigal Balshine-Earn, [1]Hans A. Hofmann

[1]*Bauer Center for Genomics Research, Harvard University, 7 Divinity Ave., Cambridge, MA, USA*

[2]*Department of Psychology, McMaster University, 1280 Main Street West, Hamilton, Ont, Canada*

Cichlid fishes of the Great Lakes in East Africa are known for their explosive radiation, diversity and phenotypic plasticity in reproductive behaviour. In Neolamprologus brichardi, a cooperatively breeding species from Lake Tanganyika, the breeding pair receives support in their care for offspring by juvenile helpers. However, some juveniles are aggressively evicted from the nest by the breeding pair. These non-helping individuals form aggregations near breeding sites. In the wild, juveniles of this species face a trade-off, as predation is higher on aggregation fish and helpers exhibit reduced growth. While behaviour, life-history and time/energy budgets exhibited by helpers have been well characterized, very little is known about aggregation fish and the underlying molecular mechanisms which characterize the two phenotypes. Our objective is to test hypotheses regarding the types and number of genes involved, the presence of gene interactions and of genetic variation for plasticity in an evolutionary context. Since gene interactions are hypothesized to be a fundamental part of complex traits, an integrative system-level approach such as DNA microarrays, allow shedding new light on these hypotheses. To contrast neural gene expression patterns of different phenotypes of N. brichardi living in a semi-natural laboratory environment, we are using a cDNA microarray containing 6000 elements from cDNA library derived from the brain of another Tanganyikan cichlid, (*Astatotilapia burtoni*), which can be used because of the phylogenetic proximity. There are two types of comparisons: 1) Among groups: helpers versus aggregation fish originating from the same brood 2) Among genotypes: individuals with the same phenotype (helpers) from different broods. We will be able to detect presence of gene interactions effect on the phenotype and to partition variation of gene expression within a phenotype between genetic and environmental components. These results will provide the basis of further experiments to determine if candidate genes are a cause (trigger of phenotypic change) or a consequence (maintenance of phenotype) of change in phenotypes.

17.9P

IS RESISTANCE FUTILE? THE ANALYSIS OF LONGEVITY AND STARVATION RESISTANCE IN SEVERAL *DROSOPHILA* SPECIES

[1,2]Egon A. Baldal, [1]Paul M Brakefield, [2]Jacques J. M van Alphen, [1]Bas J. Zwaan

[1]*Evolutionary Biology, Institute for Biology Leiden, Leiden University, Kaiserstraat 63, 2300 RA, Leiden, The Netherlands*

[2]*Animal Ecology, Institute for Biology Leiden, Leiden University, Kaiserstraat 63, 2300 RA, Leiden, The Netherlands*

Generally, selection on longevity yields highly starvation resistant flies. Therefore it is often thought that longevity and starvation resistance share a common genetic mechanism. In addition the traits are largely dependent on environmental cues during development. For *Drosophila melanogaster* one such cue is larval density. In this study we compare *D. melanogaster* with a closely related species, *D. ananassae*, and with a more distantly related species, *D. willistoni*, in their reactions to three density treatments during development. The species show intriguing differences in their life history strategies.

17.10P

ARTIFICIAL SELECTION FOR INCREASED WING LENGTH AND ITS EFFECT ON THE INTEGRATION OF OTHER COMPONENTS OF THE COMPLEX PHENOTYPE OF FLIGHT IN *DROSOPHILA MELANOGASTER.*

Phillip T. Barnes, Ryan Vachon, Betty Carreira, Aubrey Bettridge, Leslie Diaz, Anne Lane Byrd

Connecticut College, 270 Mohegan Avenue, New London, CT 06320, USA

The effect of artificial selection for increased wing length on the integration of the components of the flight morphology and physiology of *Drosophila melanogaster* was studied. Wing-beat frequency and wing-stroke amplitude, during hovering (tethered) flight, and body mass and wing size and shape were measured. These characters were analyzed separately and were also used in aerodynamic formulas to calculate the aerodynamic, inertial and total mechanical power outputs of the flight muscles. These power output calculations were considered to be a measure of the complex phenotype of flight ability. Two selection lines and two control lines were initiated from a genetically heterogeneous laboratory cage population that was at approximate genetic equilibrium for the characters. Selection lines were propagated by selecting the top 12 of 36 flies from each sex in each line in each generation, based on wing length. Control lines were propagated by randomly selecting 12 of 36 flies from each sex in each line in each generation. As of generation 34, the selection lines had diverged from the control lines: (1) with significantly greater wing length, wing area, body mass, and raw power output estimates (not adjusted for mass) and (2) with significantly lower wing-beat frequency. There was no divergence between the selection and control lines either for wing amplitude or for the mass-adjusted power output estimates. Hypotheses concerning the mechanistic behavior of the flight apparatus, either as a "simple" mechanically resonant oscillating system or as a system whose components (e.g., wing-beat frequency, wing amplitude, wing size and shape) can be adjusted evolutionarily to produce optimal mechanical power output will be discussed.

17.11P

LARVAL GENE EXPRESSION AND ADULT BODY SIZE IN NATURAL POPULATIONS OF *DROSOPHILA MELANOGASTER*

Zoltán Bochdanovits, Gerdien de Jong

Evolutionary Population Biology, Utrecht University, the Netherlands

Understanding adaptive phenotypic variation is one of the most fundamental problems in evolutionary biology. Genes involved in adaptation are most likely those that affect traits most intimately connected to fitness: life-history traits. The genetics of quantitative trait variation (including life histories) is still poorly understood, but several studies suggest that (1) quantitative variation might be the result of variation in gene expression, rather than protein evolution and (2) natural variation in gene expression underlies adaptation. The next step in studying the genetics of adaptive phenotypic variation is therefore an analysis of naturally occurring co-variation of global gene expression and a life-history trait. Here we report a microarray study addressing the co-variation in larval gene expression and adult body weight, a life history trait involved in adaptation. Natural populations of *Drosophila melanogaster* show adaptive geographic variation in adult body size with larger animals at higher latitudes. Conditions during larval development also affect adult size with larger flies emerging at lower temperatures. We found statistically significant differences in normalised larval gene expression between geographic populations at one temperature (genetic variation), and within geographic populations between temperatures (developmental plasticity). Moreover, larval gene expression correlated highly with adult weight, explaining 81% of its natural variation. Of the genes that show a correlation of gene expression with adult weight, most are involved in cell growth, cell maintenance or are associated with growth pathways.

17.12P

A JUVENILE HORMONE GENE AFFECTS LIFE HISTORY TRAITS IN *DROSOPHILA*

Thomas Flatt

University of Fribourg, Department of Biology, Unit of Ecology and Evolution, Chemin du Musée 10, CH-1700 Fribourg, Switzerland

Understanding how traits are connected to make up the whole organism remains a fundamental problem in evolutionary biology. For instance, life history theory often assumes the existence of alleles with multiple effects on fitness components. Although data on genetic covariances are often consistent with pleiotropy, there are only few examples of pleiotropic loci that validate this assumption. The Methoprene-tolerant (Met) gene in *Drosophila melanogaster* may be such a locus. Its gene product, a juvenile hormone binding protein, mediates the action of juvenile hormone (JH). This hormone is known to affect several life history traits, with recent evidence suggesting that JH mediates the trade-off between fecundity and longevity. Here I indirectly confirm the pleiotropic action of JH on life history traits. Using quantitative complementation tests, I investigated effects of Met alleles on life history traits (developmental time, onset of reproduction, and several measures of fecundity). I found that the Met locus affects several traits, suggesting that some alleles are pleiotropic and that life history traits are linked through the action of hormones.

17.13P

ESTIMATING SEX-SPECIFIC DISPERSAL RATES WITH AUTOSOMAL MARKERS IN HIERARCHICALLY STRUCTURED POPULATIONS.

[1]Pierre Fontanillas, [2]Eric Petit, [1]Nicolas Perrin

[1]*University of Lausanne, Institute of Ecology, Bat Biology, CH-1015 Lausanne*

[2]*University of Rennes I, Ethology, Evolution, Ecology, UMR 6552, F-35042 Rennes cedex*

Vitalis (2002) recently suggested that sex-specific dispersal rates can be quantitatively estimated on the basis of sex- and state-specific (pre- vs post-dispersal) F-statistics. We extend this approach to account for the hierarchical structure of natural populations, and we validate it through individual-based simulations. The model is applied to an empirical data set consisting of 536 individuals (males, females and pre-dispersal juveniles) of white-toothed shrews (*Crocidura russula*), sampled according to a hierarchical design, and typed for seven autosomal microsatellite loci. From this data set, dispersal rates show significant biases at the local scale (breeding-group level), but not at the larger scale (among local populations). Namely, males do not disperse among breeding groups within populations, but significantly so among populations, while females disperse at both levels. We argue that selective pressures on dispersal are likely to depend on the spatial scale considered. Long-distance dispersal should relate to population-dynamics- and re-colonization processes, which exert similar pressures on both sexes. Short-distance dispersal, by contrast, should respond to kin interactions (inbreeding- or kin competition avoidance), which exert differential pressure on males and females.

17.14P

THE EVOLUTION OF ALLOMETRY AMONG TRAITS WITHIN A FUNCTIONALLY INTEGRATED PHENOTYPE

W. Anthony Frankino, Paul M. Brakefield

Institute of Biology, Leiden Univeristy, The Netherlands

Functional integration among traits is predicted to favour the evolution of developmental integration among those same traits. One reason for this is that such developmental integration facilitates coordinated changes among elements of the phenotype that work together, maintaining functional scaling relationships when genetically-based or environmentally-induced changes in some traits occur. Insect forewings, hindwings, and body mass comprise a suite of traits which must scale properly, therefore these traits are expected to be developmentally integrated and to resist changes among their scaling relationships. We sought to determine the evolutionary malleability of scaling relationships within this functionally integrated suite of traits using the butterfly *Bicyclus anynana.* Artificial selection was applied to alter the allometry between fore- and hindwing area or between forewing area and body mass. Individuals were selected based on their orthogonal distance from a given allometry. After only 10 generations of selection, the allometry of each selected line had diverged ~ 2 standard deviations from the allometries of the unselected control line. No consistent pattern in the magnitude of change among individual traits that comprise each allometry was apparent, suggesting that different evolutionary paths were taken to produce convergent phenotypes. Moreover, comparison of these same traits with those of other genetic lineages of *B. anynana* reveals a surprising variability in scaling relationships, and of how this flexibility is achieved. Our results indicate that this functionally integrated trait suite is not developmentally integrated tightly. To the contrary, substantial variation is present in the development of the individual traits, and this can respond to selection applied to the scaling relationships themselves. We plan to continue selecting on the allometric relationships among the traits comprising this functionally integrated trait suite. Our aims are to measure the locomotor performance of the novel phenotypes and to study the molecular genetic basis of differentiation among lineages.

17.15P

A GENETIC BASIS FOR PHENOTYPIC PLASTICITY IN THE NEMATODE *CAENORHABDITIS ELEGANS*

Evert W. Gutteling, Joost A. G. Riksen, Joanna Reszka, Jaap Bakker, Jan E. Kammenga

Wageningen University, Binnenhaven 5, 6709 PD Wageningen, The Netherlands

Phenotypic plasticity is a common feature in many organisms and has been observed for a number of life-history traits. The genetic basis of plasticity however is still unclear and only recently progress is made by combining molecular and statistical techniques. We have used the nematode *Caenorhabditis elegans* as a model organism to investigate the genetic basis of phenotypic plasticity in life-history traits. Offspring of an intraspecific cross was selfed to the 20th generation to obtain 1000 Recombinant Inbred Lines (RILs). A subset of the RILs was genome-wide genotyped with 121 single nucleotide polymorphism (SNP) markers and phenotypically analysed for plasticity to temperature in growth and reproductive parameters. QTL-analyses indicated that plasticity is genetically regulated and consequently a trait by itself instead of a by-product of evolution.

17.16P

PHENOTYPIC PLASTICITY, PARENTAL EFFECTS, AND PARENTAL CARE IN PLANTS: SPIKE REFLECTANCE IN *PLANTAGO LANCEOLATA*.

[1]Elizabeth P. Lacey, [2]David Herr

[1]University of North Carolina, Department of Biology, 312 Eberhart, Greensboro, NC 27402, USA

[2]University of North Carolina, Department of Biology, 312 Eberhart, Greensboro, NC 27402, USA

Phenotypic plasticity, parental effects, and parental care in plants are generally treated as independent phenomena. A study of reflectance patterns in *Plantago lanceolata* suggests, however, that they can be strongly linked. Several experiments were conducted to examine 1) the degree of plasticity in reflectance/color pattern of reproductive spikes produced by *P. lanceolata*, 2) the seasonal change in pattern, 3) the genetic basis for the pattern, and 4) the effect of reflectance/color on spike temperature. Results show that: 1) reproductive spikes increase reflectance and lighten in color throughout the flowering season in North Carolina, USA, 2) spike reflectance/color is temperature-sensitive, 3) reflectance/color plasticity is genetically based, 4) lower reflectance (darker) spikes are hotter. Coupled with previously published work showing that warmer temperatures increase offspring fitness, the experiments jointly suggest that reflectance/color plasticity produces an adaptive parental effect. By modifying spike reflectance in response to external temperature, plants thermoregulate fertilization and offspring embryonic development in a way that increases offspring fitness. Plasticity may affect gametic/gametophytic selection, or it may represent a parental care trait.

17.17P

QUANTIFYING COSTS ASSOCIATED WITH EVOLUTION OF EASY BLEEDING IN LARVAL SAWFLIES

Suzanne C. Long, Paul Brakefield

EEW, Leiden University, Kaiserstraat 63, Leiden ZH 2311 GP, The Netherlands

The intimate network of associations between host plants, specialist herbivores and their predators/parasitoids creates a complex adaptive landscape that is highly variable in space and time. Larvae of the turnip sawfly *Athalia rosae* (Hymenoptera: Tenthredinidae) not only sequester toxic secondary metabolites from their host plants (Brassicaceae) but will "easy bleed" droplets of toxin-containing haemolymph, up to around 20% of body mass, in response to predator contact. This response has been demonstrated to be an effective defence against some guilds of predators (Maller & Brakefield, in prep.), but at what cost? Apart from metabolic loads associated with sequestration of toxins in the haemolymph, costs accruing from loss of water and metabolites and increased development time seem likely to be considerable. As part of the INCHECO project, we attempted to quantify the cost of the easy bleeding response in terms of metabolic rate, by respirometry of individual larvae. Changes in rates of CO2 production were detected associated with the easy bleeding response, along with shifts in associated traits as integument resistance, pupal size and development time. Substantial variation in the scale of the easy bleeding response between individuals and populations of *A. rosae* may be one of the mechanisms enabling the species to persist in temporally and spatially variable adaptive landscapes.

17.18P

HOW PREDICTABLE IS THE RATE OF CONVERGENT EVOLUTION?

[1]Margarida Matos, [1]Pedro Simùes, [2]Teresa Avelar, [3]Michael Rose, [1]Ana Duarte, [1]Raquel Gonçalves, [1]Carla Rego

[1]Fac. Ciências, Univ. Lisboa, Centro de Biologia Ambiental/Dep. Biologia Animal, Lisboa, Portugal

[2]Universidade Lusófona de Humanidades e Tecnologias, Campo Grande, Lisboa, Portugal

[3]University of California, Irvine, Department of Ecology and Evolutionary Biology, CA, USA

Though it is assumed that convergence occurs when different populations adapt to similar environments, this has rarely been shown. We studied laboratory adaptation by wild-caught *Drosophila subobscura* as a model for evolutionary convergence. We have found convergence to the values of established populations for most traits in two independent derivations from the same natural location (1992 and 1998). However, we also found that the two sets of populations differed in their rates of convergence. This was probably due to founder effects or genotype-by-environment interactions. To clarify the reproducibility of convergent evolution, in 2001 we synchronously founded two new laboratory populations, one from the usual natural location, the other from a different natural location. A comparison of the dependence of evolutionary rate on initial differentiation shows significant differences among all studies except between the two sets derived from the same location within a shorter period. Though the overall analysis suggests predictability of the rate of convergence as a function of initial states, the significant differences between studies also suggest caution when generalising between studies of evolutionary processes.

17.19P

BULGY TADPOLES: INDUCED DEFENSIVE MORPH

Kinya Nishimura, Osamu Kishida

Hokkaido University, Graduate School of Fisheries Sciences, Hakodate 041-8611, Japan

Organisms have evolved various types of defensive systems, such as chemical, behavioural, and morphological, to respond to biotic hazards. A part of or, sometimes, the entire defensive system is constitutive to the corresponding hazard, while other times, it is induced by hazard cues perceived. Morphological defenses tend to be constitutive compared with the other types of defensive systems. If organisms induce a defensive morph that enables them to deal with predation risk, the morph is constructed as soon as possible before an actual risk arises soon after receiving a pre-echo. Organisms prognose predation risk based on sonic, visual, chemical, and tactile cues. Organisms that adopt the inducible phenotype withhold energy until there is a pressing need. They do not expend energy unnecessarily and can use it for other needs in the absence of predation hazard. Inducible morphological defense is a thrift strategy which may have evolved with an adequate response to a reliable cue under the condition of unpredictably infrequent predation risk. Furthermore, unlike behaviour and substance release that require irretrievable energy, organisms possessing an inducible morph might have an option to withdraw the cost that has been invested into the morph after removal of the needs, i.e., reversibility. Here, we report on a predator-induced bulgy morph in tadpoles, the larvae of an anuran, *Rana pirica*, which prevents the predator, the larvae of a salamander, *Hynobius retardatus*, from swallowing them. The induction of bulgy morph requires proximate cues of the salamander larva. The tadpoles modify the extent of their bulginess according to their own size and immediately revert to the typical morph after the predation risk is removed.

17.20P

PHENOTYPIC PLASTICITY OF STARVATION RESISTANCE IN *BICYCLUS ANYNANA*

Jeroen Pijpe, Bas J. Zwaan, Paul M. Brakefield

Leiden University/ Institute of Biology, Kaiserstraat 63, 2311 GP Leiden, the Netherlands

The African butterfly *Bicyclus anynana* has an exceptional life history in the wild in which adult generations occur each year in very different seasonal environments. Phenotypic plasticity has evolved in these butterflies to adapt them with very different life histories in the alternative environments. The plasticity extends from wing patterns to major differences in metabolic rates, the use of glycogen versus lipid reserves, in behaviour and reproductive biology as well as in ageing curves. We use *Bicyclus anynana* as a model organism to investigate the complex phenotype of ageing in the IOP Genomics project "The genetic determination of longevity and disease at old age". The aim is to integrate the genetic information from model systems and whole genome screens to explain human longevity and disease in ageing populations. Here we present some first results associated with divergent life spans and ageing phenomena of the adult butterflies of the two seasonal forms. Populations of butterflies present in the laboratory that are selected for a 'wet season' phenotype (Real High) and a 'dry season' phenotype (Real Low) were used in an experiment to investigate the ability to resist starvation. The Stock population was used as a control. The F1 adults were randomly divided into two temperature groups (18°C and 27°C). The F2 adults from both groups were again randomly divided into the same temperature groups and subjected to starvation. Temperatures simulate both wet (27°C) and dry (18°C) seasonal conditions that the butterflies encounter in natural environments. Results indicate that dry season lines are slightly more starvation resistant, but low developmental temperatures, occurring in the dry season, have a large negative the effect on survival. These phenomena are explained by data on basal metabolic rate. Implications for survival and adaptation in the wild are discussed.

17.21P

POLLEN MORPHOLOGY DEVELOPMENT AND EVOLUTION

A. Ressayre, S. Nadot, C. Raquin, L. Pennet, P. H. Gouyon

Laboratoire ESE, Université Paris XI, bat. 362, 91405 Orsay cedex

Flowering plants produce a simple organism, the pollen grain, to disperse their male gametes. Pollen grains are constituted of a few cells surrounded by a protective wall composed of sporopollenin. Pollen wall exhibits usually one or several well-defined regions, the apertures, where the external part of the wall is reduced or absent. Aperture function as openings, permitting water uptake and the exit of the pollen tube during pollen germination. They also permit to prevent pollen breakage by accommodating pollen volume variation. Angiosperms display a wide range of variation in aperture number and distribution (the aperture pattern) at any taxonomic level including within individual plants. Aperture pattern is determined during male meiosis and appears to be tightly linked with the cytoplasmic division that leads to the formation of the microspores (that will later develop in pollen grains). Several elements that compose the developmental sequence leading to microspore separation affect aperture pattern ontogeny. Angiosperms consist of two monophyletic groups (monocots and eudicots) rooted in a basal paraphyletic group (Magnoliids). For low aperture numbers (from one to six), aperture patterns are characteristic of the major taxonomic divisions. On the basis of the aperture pattern, angiosperms are divided in two morphological groups, on the one hand magnoliids and monocots, on the other hand eudicots. In both groups, common mechanisms are involved in aperture pattern ontogeny, the differences between groups appearing to be due to differences in the way cytokinesis is completed.

17.22P

PHENOTYPIC PLASTICITY IN HOVERFLIES:EXPLORING PHENOTYPIC INTEGRATION BY HIERARCHICAL COMPARISON OF PHENOTYPIC CORRELATION MATRIXES

Hans C. Roskam, Mart M. Ottenheim

University of Leiden, PO Box 9516, NL-2300 RA Leiden

Phenotypic plasticity is an important life-history trait which can allow organisms to overcome adverse environments. Because organisms function as an integrated whole, such responses to environmental variation are expected to occur in a co-ordinated way, hence affecting extensive suites of characters. This postulate is known as 'phenotypic integration', and was coined in order to compare such complex responses in related taxa. Genetic (G)- and/or phenotypic (P) variance-covariance matrixes reflect this coherence of character change. The significance of a comparison of phenotypic plasticity in related taxa is obvious within an evolutionary context because such comparison will not only shed light on the process of adaptation but also give insight into the historical dimension of plasticity as life-history trait: did plasticity recently evolve under present selection or was is acquired in the past and inherited from ancestors? A statistical basis for comparison of phenotypic integration, however, awaited the development of multivariate testing procedures. Common principal component analysis is able to test differences between covariance matrixes in a hierarchical fashion: not only equality and proportionality in terms of eigenvalues are detected, but the algorithm also allows the detection of common eigenvectors (principal components). The potential to analyse more complex relationships among matrixes may provide an important tool in order to address questions concerning the impact of evolutionary processes on change in covariance pattern. It is unclear how stable matrixes remain when environmental variation is introduced either within a natural or an experimental context. Our present aim is to analyze how sensitive covariance patterns are to environmental variation and to understand the change in covariance patterns within an evolutionary context. Our data concern a hoverfly study system.

17.23P

THE COST OF MELANIZATION: BUTTERFLY WING COLORATION UNDER ENVIRONMENTAL STRESS

[1]W. Talloen, [1]H. Van Dyck, L. Lens

[1]University of Antwerp, Laboratory of Animal Ecology, Universiteitsplein 1, 2610 Wilrijk, Belgium

[2]Ghent University, Terrestrial Ecology Unit, Belgium

Evolutionary studies of organismal design typically focus on relationships between morphology and ecology, and infer results in an adaptive framework. However, adaptive variation can only occur within the boundaries imposed by constraints, like developmental constraints. Under resource-limited conditions, the costs associated with the development of an adaptive trait may therefore contribute significantly to observed phenotypic variation in the field. This source of non-adaptive variation has often been ignored, for instance in the field of inter- and intraspecific variation in degree of butterfly wing melanization. Butterfly wing coloration is functional significant in multiple ways, including thermoregulation, crypsis, predator deflectance, sexual signalling and, obviously, flight. Being flying heliotherms, higher degrees of wing melanization have been shown to be adaptive in colder environments. Associated costs of increased melanism have received far less attention. As melanin is a complex polymer, its synthesis may be constrained if ambient conditions limit the energy budget of development. This hypothesis was tested by comparing melanization among Speckled wood butterflies *Pararge aegeria* that fed as a larvae on host grasses experiencing different drought-stress treatments. Treatment differences were validated both at the level of the host plant and of the butterfly. Melanization rate was measured as average gray value of the basal dorsal wing area, which is known to be functionally significant for basking in order to thermoregulate. Individuals reared on drought-stressed host plants developed paler wings, while darker individuals developed slower and less stable as estimated by their level of fluctuating asymmetry. These results provide evidence that melanin is indeed costly to synthesize, and that differences in environmental quality can induce phenotypical variation in wing melanization. Therefore, studies dealing with spatial and/or temporal patterns of variation in wing melanization should not only focus on adaptive explanations alone, but rather on a cost-benefit balance under particular sets of environmental conditions.

17.24P

EXPERIMENTAL REVERSE EVOLUTION: FROM FITNESS TO MOLECULAR VARIATION AT CANDIDATE GENE LOCI

Henrique Teotónio

Laboratory of Evolutionary Genetics, Instituto Gulbenkian de Ciência, Oeiras, Portugal

Reverse evolution has been studied in *Drosophila melanogaster* populations with an experimental evolution approach. An exhaustive description of life-history phenotypic evolution has been done and a study on the genetic basis of evolutionary responses conducted. We found that reverse evolution occurs but is contingent on previous evolutionary history. The extent to which molecular reverse evolution shows the same patterns as phenotypic reverse evolution is not clear, particularly for sexual species. We present preliminary data on the extent of linkage disequilibrium among molecular markers at a candidate gene locus region, copper-zinc superoxide dismutase, for both ancestral and differentiated populations, as a necessary first step for an understanding of the role of selection and drift during reverse evolution at the molecular level.

17.25P

WHAT IS THE ROLE OF RECOMBINATION IN THE GENERATION OF NEW S-LOCUS SPECIFICITIES?

[1]Cristina P. Vieira, [2]Deborah Charlesworth, [1]Jorge Vieira

[1]Instituto de Biologia Celular e Molecular, Rua do Campo Alegre 823, 4150-180 Porto, Portugal

[2]Institute of Cell, Animal and Population Biology, University of Edinburgh, Edinburgh EH9 3JT UK

The gametophytic self-incompatibility system found in plants of the Solanaceae, Rosaceae, and Scrophulariaceae families all use a highly polymorphic gene at the S-locus, called the S-RNase gene, to control the pistil's ability to recognize and reject self-pollen. The S-locus had been thought to be exposed to little if any recombination to maintain tight linkage between the S-RNase gene and the pollen S gene. Evidence suggesting intragenic recombination at the S-locus has, however, been obtained from the analyses of closely related alleles of the S-RNase gene in a natural population of *Petunia inflata* (Solanaceae). It is thus possible that recombination, as well as mutation, may contribute to the generation of new S-locus specificities. In order to address this issue we have examined published sequence data from the S-locus in several species of the Solanaceae, Rosaceae and Scrophulariaceae families. The relationship between linkage disequilibrium between sites in the locus and physical distance between the sites suggests rare intragenic recombination in the evolutionary history of four species of Solanaceae and two species of Rosaceae. It is not clear whether similar sequences experience much higher recombination rates than highly divergent ones. Even rare recombination could, however, be an important factor in the evolution of these loci. In Rosaceae, there is no data implying a centromeric localisation of the S-locus, a region with suppressed recombination levels over a wide taxonomic range including plants. Intragenic recombination in species of this family may thus be an important factor in the generation of new S-locus specificities. In order to address this issue we are determining the DNA sequences of S-alleles from natural populations of *Prunus spinosa*.

17.26P

CONVERSION OF EPISTATIC VARIANCE DURING EVOLUTION BY DIRECTIONAL SELECTION

Jason Wolf

University of Tennessee, Dept. of Ecology & Evolutionary Biology

There have been a number of theoretical analyses examining the conversion of epistatic to additive variance during drift events (e.g., during population bottlenecks). These models assume that a trait is neutral and that its evolution is governed solely by drift. However, an interest in epistatic and additive genetic variances usually stems from an interest in the evolutionary potential of traits, with the implied assumption that these traits are not necessarily neutral. In this talk I present an analysis of the conversion of epistatic to additive variance during evolution by selection. The rate at which the epistatic interaction between loci releases additive variance to fuel directional evolution is examined. The role of linkage disequilibrium created by selection is also explored.

17.27P

ARTIFICIAL SELECTION ON LIFE HISTORY CO-VARIATION IN *BICYCLUS ANYNANA*: CONSTRAINTS, GENETICS AND HORMONE PHYSIOLOGY

Wilte G. Zijlstra, Marc J. Steigenga, Paul M. Brakefield, Bas J. Zwaan

Institute of Biology, Leiden University, Kaiserstraat 63, 2311 GP Leiden, The Netherlands

Responses to natural selection can be severely hampered by (genetic) correlations among a suite of traits. Such a constraint can be studied using antagonistic selection experiments, that is, two-trait selection in opposition to this correlation. The two traits studied here were development time and wing pattern (eyespot size) in *Bicyclus anynana*, both of which have a clear adaptive significance and are integrated in the life history of this seasonal butterfly. Rates of response were higher for eyespot size than for development time, but were independent of the concurrent selection (either in the same direction as the correlation or perpendicular to it). Regimes differed in both traits in all directions after 11 generations of selection. The antagonistic (uncoupling) lines had higher responses relative to predicted than the synergistic lines in development time, and equal relative responses in eyespot size. The response of the uncoupling lines was not hampered by a lack of selectable genetic variation and the relative response in the development time was larger than expected based on response in the coupled direction and quantitative genetic predictions. Both developmental time and eyespot size are mediated by the insect hormone ecdysone. Variation in ecdysone titres and signalling may thus form the physiological basis of the correlation between the two traits. Hence, we also investigated the dynamics of the insect hormone ecdysone by measuring haemolymph titres and response to hormone injections. Interestingly, ecdysone biology is only affected by selection for developmental time, and not by selection for eyespot size. Our data suggests that the structure of the genetic architecture does not constrain the short term, independent evolution of both wing pattern and development time. Moreover, although the insect hormone ecdysone affects both traits, its mode of action is apparently uncoupled in the newly selected phenotypes.

Symposium 18

The evolution of sexual size dimorphism

Organisers: Jutta Schneider & Marie Herberstein

Roger Stevens Lecture Theatre 20

09.20 – 09.50	**Blanckenhorn, W. U.** Selection, Rensch's rule and the evolution of sexual size dimorphism in dung flies
09.50 – 10.20	**Badyaev, A. V.** Male and female growth in sexually dimorphic vertebrates: Harmony, conflict, or both?
10.20 – 11.00	**Coffee**
11.00 – 11.20	**Szekely, T.** Sexual selection explains Rensch's rule of size dimorphism in shorebirds
11.20 – 11.20	**Höglund, J.** The evolution of sexual size dimorphism in grouse- phylogenetic data and the molecular basis for sex specific growth patterns in chicken
11.40 – 12.00	**Teder, T.** Females tend to vary more in body size than males: a meta-analysis
12.00 – 12.20	**Fairbairn, D.** Deducing the adaptive significance of divergent genitalic and somatic sexual size dimorphism in a water strider
12.20 – 12.40	**Uhl, G.** Sex related growth strategies in a spider
12.20 – 14.00	**Lunch**

Invited Speakers

18.1

SELECTION, RENSCH'S RULE AND THE EVOLUTION OF SEXUAL SIZE DIMORPHISM IN DUNG FLIES

Wolf U. Blanckenhorn

Zoological Museum, University of Zürich, Switzerland

Body size is one of the most important quantitative traits under evolutionary scrutiny, and sexual size dimorphism (SSD) is common in organisms. The selection equilibrium model states that SSD of a given species is the net evolutionary result of sex-specific selection pressures — sexual selection in males, fecundity selection in females, and viability selection in both sexes — within the limits set by phylogenetic, genetic, developmental and physiological constraints. Using two dung fly species with contrasting SSD as model systems, I first discuss the micro-evolutionary effects of current patterns of selection on body size at the within-population, ecological level. This approach is then extended to explain the macro-evolutionary pattern of hypo- (or negative) allometry for SSD (i.e. greater variation in male than female size = Rensch's rule), first among populations of the same species and then among closely related species. I conclude that strong sexual selection for large male size may explain the current SSD (males larger) in the yellow dung fly *Scathophaga stercoraria* (Diptera: Scathophagidae), and variation in the intensity of sexual selection on body size may even explain Rensch's rule among populations and among closely related species. However, this is not true for the black scavenger fly *Sepsis cynipsea* (Diptera: Sepsidae; females larger). In particular, we still lack evidence for viability (and other) selection counteracting the strong fecundity and mating advantages of large size in these insects.

18.2

MALE AND FEMALE GROWTH IN SEXUALLY DIMORPHIC VERTEBRATES: HARMONY, CONFLICT, OR BOTH?

Alex. V. Badyaev

University of Arizona, 1041 E. Lowell, Tucson, AZ 85721-0088, USA

In most vertebrates, males and females are nearly identical in morphology during early development, but as a result of highly divergent growth and organism-wide reorganization achieve remarkably different adult morphologies. Although numerous studies have documented selection pressures that favour distinct morphologies of adult males and females, we know very little of the mechanisms that enable the virtually genetically identical sexes to end up so different in morphology. I will address the contrast between the striking diversity of ontogenetic processes that produce dimorphism and the highly conserved genetic variation in adult dimorphism. Recent studies emphasize the importance of a developmental approach by showing that rapid evolution of sex-specific ontogenies can produce sexual dimorphism whilst maintaining the integrity of the developmental program that is shared between the sexes.

Contributed talks

18.3

SEXUAL SELECTION EXPLAINS RENSCH'S RULE OF SIZE DIMORPHISM IN SHOREBIRDS

[1]**Tamas Szekely**, [2]Robert P. Freckleton, [3]John D. Reynolds

[1]*Department of Biology and Biochemistry, University of Bath, Bath BA2 7AY, UK*

[2]*Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK*

[3]*Centre for Ecology, Evolution and Conservation, School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK*

The extent of sexual size dimorphism relates to body size in many animals including insects, reptiles, birds and mammals: large species have male-biased dimorphism, whereas small species are not dimorphic or exhibit female-biased dimorphism (Rensch's rule). Sexual selection has been hypothesised to explain Rensch's rule, yet the specific nature of this selection has remained elusive. Here we show that Rensch's rule is determined by two components of sexual selection in shorebirds and allies (Charadrii): the intensity of sexual selection acting on males, and the agility of males' display. These variables have interactive effects so that the effect of the intensity of sexual selection on dimorphism depends on male agility. We suggest that the association between sexual size dimorphism (both male-biased and female-biased dimorphisms) and body size expressed as Rensch's rule is determined in many animals by a single set of evolutionary explanations: the intensity of sexual selection as modulated by the agility of males' display. Our results also show that studies using sexual size dimorphism as an indicator of the intensity of sexual selection are invalid.

18.4

THE EVOLUTION OF SEXUAL SIZE DIMORPHISM IN GROUSE- PHYLOGENETIC DATA AND THE MOLECULAR BASIS FOR SEX SPECIFIC GROWTH PATTERNS IN CHICKEN

Jacob Höglund

Population Biology/EBC, Uppsala University, Norbyv. 18D, SE-752 36, Uppsala, Sweden

Grouse (subgenus- Tetraoninae) display extensive interspecific variation of sexual size dimorphism. Furthermore, several independent studies have established and corroborated robust phylogenetic hypotheses for this group of birds. Two general patterns emerge from phylogenetic analyses of size dimorphism: 1) The level of sexual size dimorphism is correlated with polygyny level such that polygynous species are more size dimorphic than less polygynous. 2) Larger species are more size dimorphic than smaller species. This implies that sexual selection for larger males within species have taken females further off a hypothetical ecological optimum. It further implies that what has been selected is larger size in males which has led to initial corresponding evolutionary responses in females. However, as selection has become more intensive corresponding sex specific growth patterns may have evolved. I review available studies on QTL-mapping of growth in chicken. These studies show that most of the difference in body size between the sexes is established between hatching and 200 days past hatching and that a QTL show pleiotropic effects between feeding efficiency and growth. Although QTL studies have not yet involved the sex chromosomes it is possible that genetic modifiers determining growth may be sex-linked. As envisaged by Rice (1984), genetically determined sexually antagonistic modifiers of growth, possibly linked to the sex chromosomes, may play an important role in the expression of sexual size differences.

18.5

FEMALES TEND TO VARY MORE IN BODY SIZE THAN MALES: A META-ANALYSIS

Tiit Teder

Estonian Agricultural University, Institute of Zoology and Botany, Riia 181, Estonia

Various hypotheses have been proposed to predict variance in the values of different traits. Traits closely associated with fitness (e.g. body size, fecundity, longevity) have deserved special attention in this context. There is, however, no general consensus whether these traits have lower or higher variances as compared to other traits. The canalisation hypothesis predicts that traits having stronger impact on fitness have a lower degree of variation. The variance accumulation hypothesis, on the contrary, suggests that traits closely related to fitness are the most variable ones. Instead of regarding these hypotheses as mutually exclusive alternatives, a more reasonable approach might be to ask for which species, and why, would one of these explanations be more relevant. An alternative to comparing variances of different traits could be comparing variances of the same trait between males and females. Such an approach has specific advantages. In particular, in most animals males and females share common environment and developmental patterns during their preimaginal stages. Fitness consequences of body size is what differ between the sexes. Surprisingly, however, this opportunity to reveal variance-determining mechanisms has not been used yet. In the present study, we conducted a meta-analysis to reveal patterns of sex-specific variance of body size in insects. Moreover, we studied if the patterns differ depending on taxon, life-history strategies, sexual size dimorphism etc. The analysis is based primarily on original studies that have reported body weight (and a statistic describing variance of body weight) for males and females separately. The analysis showed a weak but significant tendency of female body size being more variable than that of males. The result was consistent in most insect orders and major feeding guilds. The general pattern and major exceptions of it are discussed.

18.6

DEDUCING THE ADAPTIVE SIGNIFICANCE OF DIVERGENT GENITALIC AND SOMATIC SEXUAL SIZE DIMORPHISM IN A WATER STRIDER.

Daphne Fairbairn

Department of Biology, University of California, Riverside, California 92521, USA

Sexual selection and sexual conflict have played an important role in the evolution of sexual dimorphism in water striders. In the stream-dwelling water strider, *Aquarius remigis* (Say), sexual selection acting through differential mating success tends to favour larger males. However, detailed measures of sexual selection in natural populations indicate that this selection actually favours males with smaller somatic components but larger genitalia. Sexual selection favouring a smaller body size is consistent with the female-biased size dimorphism characteristic of the Gerridae, while selection favouring longer external genitalia is consistent with the observed shape dimorphism between the sexes. We present quantitative genetic evidence that external genital length is heritable and only weakly correlated with somatic body size, a pattern of genetic architecture that should facilitate rapid response to divergent selection between somatic and genitalic size. To deduce the adaptive significance of large external genitalia, we use video analysis plus light and scanning electron microscopy to describe genitalic function during mating interactions, phallus inflation and intromission. These analyses suggest that long external genital segments increase the ability of males to achieve intromission in spite of active female resistance, to maintain intromission during the prolonged copulations characteristic of this species, and to displace and destroy sperm already present in the female's reproductive tract. We conclude that the sexual selection contributing to the observed pattern of size and shape dimorphism in *A. remigis* derives from a complex mix of direct male/male competition for mating opportunities, sexual conflict, and internal sperm competition, with selection acting differentially on body and genital components.

18.7

SEX RELATED GROWTH STRATEGIES IN A SPIDER

Gabriele Uhl, Sandra Schmitt, Martin A. Schäfer

University of Bonn, Department of Neurobiology, Endenicherallee 11-13, 53115 Bonn, Gernany

Maturation time and size at maturation are highly important for reproductive success in many species. The benefits, however, may differ between the sexes. In females, both parameters seem fertility selected, whereas in males maturation time and size strongly depend on the mating system. We performed staged matings between pairs of the spider *Pholcus phalangioides*, a species with slightly larger males than females, and followed female oviposition behaviour and hatching success of clutches over 140 days, comparable to the natural reproductive season. We found that female size was positively related to the number of offspring produced and to hatching success but not to the number of oviposition events. To study reaction norms of growth we reared the offspring from the first clutch under two food levels to sexual maturity. We determined maturation time, size and mass off offspring. There was a strong effect of food level on size of female and male offspring. However, female mass and maturation time was independent of the feeding regime, whereas males matured with less weight and later on low food level. Our study demonstrates that selection on male size seems stronger than selection on male mass, whereas in females mass seems to be more important than size. Female growth strategies seem to be fertility selected whereas male strategies seem to be sexually selected as it was shown that male size affects the chance of monopolizing a partner. That there is a strong selective advantage for large males seems corroborated by the finding that parent size had an effect on the size and mass of male but not female offspring.

Posters

18.8P

DOES A GENERAL MODEL FIT TO EXPLAIN MOULTING STRATEGIES IN LEPIDOPTERAN LARVAE

Toomas Esperk, Toomas Tammaru

Institute of Zoology and Botany, Riia 181, EE-51014 Tartu, Estonia

Limited attention has been paid to discrete instars of arthropods in life history models. It is not clear when and why should a larva moult. J.M.C. Hutchinson and co-workers (1997) have proposed a model for the optimal growth and moulting strategies for animals with a discontinuous growth schedule. These authors assume that the main advantage of larval moult is in allowing heavily sclerotized inextensible parts of the body (such as jaws) to increase in size. These structures grow discontinuously only in connection with larval moults. It is further assumed that the size of these inflexible structures determines the rate of food acquisition and thereby growth rate of an organism. However, these authors admit that empirical basis to evaluate these assumptions is scarce, and stress the need for further experimental work. The aim of the present study was to test the validity of the assumptions of the Hutchinsons model. Data to test for these hypotheses were obtained from laboratory rearings of two lymantriid moth species. As the results of our experiment did not confirm the assumptions of the Hutchinson's model, there may be a need to reformulate the model for the case of lepidopteran larvae. In the case of an insect species whose larval instar number is not fixed, larvae which have "additional" instars grow remarkably larger than those with fewer instars. As in both species studied female larvae typically have more instars than males, the results of present experiment are important in the perspective of sexual size dimorphism.

18.9P

THE EVOLUTION OF SEXUAL DIMORPHISM IN DIURNAL BIRDS OF PREY: SEXUAL OR NATURAL SELECTION?

Jordi Figuerola, Juan Manuel Grande

Department of Applied Biology, Estacion Biologica de Doñana, CSIC, Avda. Maria Luisa s/n, E-41013 Sevilla, Spain

Birds of prey present an important interspecific diversity in the strength of sexual size dimorphism. While in some species sexes are very similar in size, in others females are the larger sex. This pattern is uncommon among birds, where males use to be the larger sex. A number of hypotheses have been proposed, although its validity has never been tested under an evolutionary approach. In a comparative analysis including 99 species of raptors we tested eight of these hypotheses. Patterns of dimorphism were unrelated to the defence of a feeding territory, and species with females larger than males did not start egg laying early, nor produced larger clutches. Patterns of incubation and nest defence were also unrelated to size dimorphism. Mating system also failed to explain a significant amount of variation in sexual size dimorphism. Our preliminary analyses supported two different hypotheses: female biased dimorphism predominated in species with males performing more acrobatic sexual displays and in species with an important bird component in the diet. Consequently, female biased dimorphism among raptors can be the result of selection for more agile males.

18.10P

THE MISMEASURE OF LIZARD: OCCAM´S RAZOR CUTS OFF PANSELECTIONIST EXPLANATIONS OF SEXUAL DIMORPHISM IN BODY SHAPE

[1]Lukáš Kratochvíl, [1]Michael Fokt, [2]Ivan Rehák, [1]Daniel Frynta

[1]Charles University, Viniènά 7, CZ-128 44 Praha 2, the Czech Republic

[2]Prague Zoo, U Trojského Zámku 3, CZ-171 00 Praha 7, the Czech Republic

Male-biased sexual dimorphism in head, limb and tail scaled to snout-vent length (SVL) has been commonly reported in many lizard species. Consequently, various hypotheses have been proposed to explain observed body shape dimorphism. The majority of them suppose that proportions of component body segments are adaptively related to sexual differences in ecology as well as in reproductive behaviour. Our study shows an alternative, much more parsimonious, explanation in the common lizard (*Lacerta vivipara*). According to our analyses, the exaggeration of a single trait, specifically trunk length in females, may explain the whole pattern of sexual differences in body shape. The only consistent adaptive hypothesis is then a reproductive advantage to females with larger abdominal cavities and consequently longer trunks. Size-adjusted heads, limbs and tails traditionally reported as bigger in males than in females and ascribed to numerous evolutionary mechanisms thus appear to be just an artifact caused by inappropriate scaling to sexually dimorphic trait (SVL). As the scaling to a single trait has been routinely used in many studies carried out in animals, we warn against quick interpretations based on such analyses and recommend more cautious inspection of allometries.

18.11P

EVOLUTION OF SEXUAL DIMORPHISM IN EUBLEPHARID GECKOS (SQUAMATA: EUBLEPHARIDAE): THE INFLUENCE OF SEXUAL OR FECUNDITY SELECTION?

Lukáš Kratochvíl, Daniel Frynta

Charles University, Vinièná 7, CZ-128 44 Praha 2, the Czech Republic

Lizards of the family Eublepharidae exhibit interspecific diversity in body size, sexual size dimorphism (SSD), head size dimorphism (HSD), occurrence of male combat, and presence of male precloacal pores. Hence, they offer an opportunity for tests of different hypotheses for the evolution and maintenance of sexual dimorphism. Historical analysis of male agonistic behaviour indicates that territoriality is ancestral in eublepharid geckos. Within Eublepharidae, male combat disappeared twice. In keeping with predictions from sexual selection theory, both events were associated with parallel loss of male-biased HSD and ventral scent glands. Eublepharids thus give new evidence that male-biased dimorphic heads are weapons used in aggressive encounters and that ventral glands probably function in territory marking rather than in intersexual communication. Male-biased SSD is a plesiomorphic character and was affected by at least three inversions. Shifts in SSD and male combat were not historically correlated. Therefore, other factors than male rivalry appear responsible for SSD inversions. Eublepharids demonstrate the full scope of Rensch´s rule, i.e. small species tend to be female-larger, larger species male-larger. All species have invariant clutches of two eggs. Within species, clutch mass correlate with female mass. However, eggs of larger species are smaller as a proportion of female mass than eggs of smaller species. Most plausibly, SSD pattern hence seems to reflect body size variation and allometry of reproduction.

18.12P

SEXUAL CONFLICT PREDICTS SEX-SPECIFIC INVESTMENT INTO BODY PARTS UNDER HIGH AND LOW POPULATION DENSITY IN A SPIDER

[1]Alexei A. Maklakov, [2]Y. Lubin

[1]Ben Gurion University, Department of Life Sciences, Beer Sheva, Israel

[2]Ben Gurion University, Department of Life Sciences, Sede Boqer, 84990, Israel

In a spider *Stegodyphus lineatus*, infanticidal males fight with egg-guarding females over mating opportunities. Winning males destroy the eggs and mate with the female to sire half of the offspring in the replacement clutch. The outcome of the fight is influenced by the cephalothorax size of the contestants. The investment in armament - the cephalothorax, may be traded-off against the investment in abdomen size, reducing female fecundity and male longevity. The pay-offs to both sexes will depend on their encounter rate, which is assumed to be a function of population density. Both sexes are expected to adjust their resource allocation into different body parts accordingly. We tested this hypothesis in two genetically distinct populations of *S. lineatus*, which are characterised by extremely different population densities. We found that: 1) males had larger cephalothorax/body size ratio than females; 2) males from a low density population had larger cephalothorax/body size ratio relative to males from a high density population; 3) females from a high density population had larger cephalothorax/body size ratio than females from a low density population. The results are in accordance with predictions derived from sexual conflict theory, and suggest the existence of an interaction between sexual conflict and life history traits.

18.13P

SEXUAL SIZE DIMORPHISM IN NEMATODES CORRELATES WITH HYPODERMAL PLOIDY LEVELS AND IS CONTROLLED BY TGF-BETA-LIKE FACTOR DBL-1

Alberto G. Sáez, Anthony J. Flemming, Encarnación Lozano, Armand M. Leroi

Imperial College London, Dept. Biological Sciences, Silwood Park Campus, Ascot, Berkshire SL5 7PY, United Kingdom

In nematodes, females or hermaphrodites are usually larger than males. As it happens with body size differences among many nematode species, these differences positively correlate with ploidy levels of hypodermal nuclei. In the nematode model organism C. elegans, and in contrast to the situation in mammals, gonadal signals do not appear to be responsible for either sexual differences in hypodermal ploidy or sexual size dimorphism. Instead, molecular signalling through a TGF-beta-like factor, DBL-1, is, at least partially, responsible for both phenomena.

18.14P

NO COSTS OF LARGE BODY SIZE IN FEMALE *ORGYIA* SPP. (LEPIDOPTERA, LYMANTRIIDAE): LARGER IS ALWAYS BETTER

[1]Toomas Tammaru, [1]Toomas Esperk, [2]Ignacio Castellanos

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

[2]*University of Maryland, Department of Entomology, College Park, MD 20742, USA*

Strong correlation between female body size and potential fecundity is often observed in insects. Directional selection favouring increased body sizes is thus predicted in the absence of opposing selection pressure. The evolutionary forces capable of counterbalancing such a 'fecundity advantage' are poorly documented. This study (Oecologia 133: 430-438) focuses on revealing the costs of large body size in the wingless females of *Orgyia antiqua* and *O. leucostigma*, two related species of lymantriid moths. Extreme behavioural simplicity of these animals allows systematic assessment of various fitness components in conditions close to natural. A linear relationship between pupal weight and potential fecundity was observed. This association was found to be independent of particular rearing conditions. There was no evidence that the relationship between fecundity and body mass becomes asymptotic with body sizes increasing. No component of fitness showed a negative phenotypic correlation with body size, some displayed a weak positive one. In particular, pupal mortality, adult longevity, mating and oviposition success, as well as egg hatching rate and egg size were established as independent on body size in a series of field and laboratory experiments. There was a very high overall efficiency of converting resources accumulated during the larval stage to egg masses. With no costs of large adult size, selective forces balancing the fecundity advantage should operate in the course of the immature development. The strong dependence of realized fecundity on female body size is considered characteristic of the capital breeding strategy (Oikos 77: 561-564), and may explain pronounced sexual dimorphism often observed in such insects.

Symposium 19

From cell to society: conflict and cooperation at different evolutionary levels

Organisers: Francis Ratnieks & Tom Wenseleers

Roger Stevens Lecture Theatre 21

09.20. – 09.50	**Szathmary, E.** Major transitions in evolution: Information, energy, boundary
09.50 – 10.20	**Frank, S. A.** Repression of competition and the evolution of cooperation
10.20 – 11.00	**Coffee**
11.00 – 11.20	**Foster, K.** How is cheating maintained in the slime mould, *Dictyostelium discoideum*?
11.20 – 11.40	**Ratnieks, F. L. W.** Conflict resolution by worker policing in insect societies
11.40 – 12.00	**Aanen, D. K.** Genomic conflicts in mushrooms
12.00 – 12.20	**Dijkstra, M. B.** The regulation of worker reproduction in queenright *Acromyrmex* leafcutter ants
12.20 – 12.40	**Korb, J.** The evolution of cooperation in termites
12.40 – 14.00	**Lunch**

Invited talks

19.1

MAJOR TRANSITIONS IN EVOLUTION: INFORMATION, ENERGY, BOUNDARY

Eors Szathmary

Collegium Budapest, 2 Szentharomsag utca, H-1125 Budapest, Hungary

Major transitions in evolution are characterized by a few phenomena that are sufficiently common, if not universal: (i) formation of higher-level evolutionary units; (ii) evolution of novel inheritance systems; and (iii) combination of function/division of labour (synergy). Local interactions seem to be important for the evolutionary dynamics of the transitions, whereas central control and contingent irreversibility often render reversal difficult. I shall take a fresh look at these issues by following Gánti's insight about the nature of living entities; namely, that they minimally must be composed of three subsystems: one for information/control, one for metabolism and one for providing some form of physical boundary. I shall review transitions in the latter two subsystems.

19.2

REPRESSION OF COMPETITION AND THE EVOLUTION OF COOPERATION

Steven A. Frank

Dept Ecology and Evolutionary Biology, Univ. of California, Irvine, CA 92697-2525, USA

Repression of competition within groups joins kin selection as the second major force in the history of life shaping the evolution of cooperation. When opportunities for competition against neighbors are limited within groups, individuals can increase their own success only by enhancing the efficiency and productivity of their group. Thus, characters that repress competition within groups promote cooperation and enhance group success. This important idea developed slowly and in a haphazard way over several years. Separate analyses have been developed for repression of competition between chromosomes within genomes, between bacterial symbionts within hosts, between worker insects within social colonies, and between humans in the emergence of complex societies. I bring out the common, general principles and the special attributes of particular cases. With the essential ideas made clear, I use hindsight to make sense of the history of this subject. Finally, I discuss several active topics of study.

Contributed talks

19.3

HOW IS CHEATING MAINTAINED IN THE SLIME MOULD, *DICTYOSTELIUM DISCOIDEUM*?

Kevin Foster, Tom Platt, Joan Strassmann, David Queller

Ecology and Evolution, Rice University, Houston, Texas 77005

The majority of multicellular organisms seem to have solved the problem of within-organism conflict by ensuring that their cells are genetically identical. The slime mould, *D. discoideum*, however, forms a multicellular organism by aggregation and genetically different cells can occur within the same organism. When starving, amoebae aggregate to form a slug that migrates and develops into a fruiting body in which 20% of cells die to form a stalk. Furthermore, some clones cheat in the fruiting body by forming more spores than is fair. This raises the question of why the cheats do not go to fixation resulting in the loss of the cheating phenotype. We will present data on two alternative explanations. First, do cheats suffer costs that counter the benefit of cheating? Second, is cheating facultative with different clones cheating under different environmental conditions?

19.4

CONFLICT RESOLUTION BY WORKER POLICING IN INSECT SOCIETIES

Francis L.W. Ratnieks, Tom Wenseleers

University of Sheffield, Dept. of Animal & Plant Sciences, Western Bank, Sheffield S10 2TN, UK

In human society, at many times and in many places, conflicts have been resolved by brute force and the dictatorial power of the tyrant. In social insect colonies, however, conflicts are resolved in a much more democratic way; not by dictatorial power or in fact, any type of central authority. Instead, their conflicts are suppressed through a self-organised system of social policing. In bees, wasps and ants, for example, worker policing by egg eating prevents worker-laid eggs from being reared. Worker policing by aggression towards individual workers trying to reproduce also occurs, and is particularly important in queenless ponerine ants. In queenless ants the colony is headed by a mated worker. All the females are totipotent and this leads to conflicts over breeder replacement. Policing by workers may also be used to force immature females to develop into workers rather than queens. The importance of policing is not just that it directly represses selfish actions – using novel theory we show that it also makes it unprofitable for individuals to act selfishly in the first place. This we term acquiescence. Acquiescence can explain, for example, why so few honey bee workers attempt to reproduce. Worker policing is widespread in insect societies, both taxonomically and in the range of conflicts that it suppresses. By helping to resolve conflicts among members of the same society, worker policing has probably facilitated the evolution of large and complex insect societies.

19.5

GENOMIC CONFLICTS IN MUSHROOMS

[1]**Duur K. Aanen**, [2]Thomas W. Kuyper, [3]Alfons J. M. Debets, [3]Rolf F. Hoekstra

[1] *Department of Population Ecology, Universitetsparken 15, 2100 Copenhagen Denmark,*

[2]*Sub-Department Soil Quality, Wageningen University, Dreijenplein 10, 6703 HB Wageningen, The Netherlands*

[3]*Laboratory of Genetics, Wageningen University, Arboretumlaan 4, 6703 BD Wageningen, The Netherlands*

Heterothallic mushrooms (hymenomycetes, Basidiomycotina) accomplish sex by exchanging nuclei without cytoplasm. In a typical life cycle hyphal fusions occur between monokaryons (haploid mycelia arising after spore germination) and subsequent reciprocal migration of the haploid nuclei without cytoplasmic mixing. The resulting dikaryon is therefore a cytoplasmic mosaic with uniformly distributed nuclei (two in each cell). Because cytoplasms of the two parents are not mixed, cytoplasmic inheritance is 'doubly uniparental': both monokaryons involved in a mating can potentially transmit their cytoplasm to the sexual spores, but normally only a single type per spore. In such a life cycle within-cell conflict between mitochondria is limited (heteroplasmy only occurs in the fused cells). However, at the organism level, within the dikaryon, mitochondria conflict over transmission, because the mitochondria transmitted to the spores are those in the mycelial region where the mushroom develops. Therefore, the conditions for genomic conflict to occur are there: natural selection acts differently at different levels. At the mitochondrial level natural selection is expected to favour mutants that increase a mitochondrion s transmission rate (e.g. by increased growth rate or by early induction of fructification). This might have deleterious effects at the individual (dikaryon) level. Therefore, at this level natural selection will act against such selfish mitochondria. Here we investigate the strategies mitochondria and nuclei can play and the conditions under which the theoretically predicted conflicts are important. We review the existing literature for evidence of the actual occurrence of the theoretically predicted conflicts.

19.6

THE REGULATION OF WORKER REPRODUCTION IN QUEENRIGHT *ACROMYRMEX* LEAFCUTTER ANTS

Michiel B. Dijkstra, Jacobus J. Boomsma

University of Copenhagen, Universitetsparken 15, 2100 Copenhagen East, Denmark

In most eusocial ants, bees, and wasps, workers are able to lay eggs but cannot mate. Because of the haplodiploid sex-determination system common to all Hymenoptera, these eggs always become males. The leafcutter ants (genera *Acromyrmex* and *Atta*) are among the few social insect groups known to have obligate highly multiple mating of the queens. As a result, workers are more closely related to the sons of the queen than to the sons of the average worker. Worker policing, similar to the worker policing behavior known from honeybees and vespine wasps, is therefore predicted in the leafcutter ants. In our earlier work with ovarian dissections we showed that, while *Atta* workers are completely sterile, approximately 1% of the workers in queenright colonies of *Acromyrmex echinatior* and *Ac. octospinosus* lay fertile eggs. Because of the high number of workers per colony, workers are potentially able to produce all the males in the colony. However, earlier genotyping of adult *Acromyrmex* males has indicated that most males are queen-derived in queenright colonies of *Ac. echinatior* and *Ac. octospinosus*. The existence of a worker policing mechanism is therefore strongly suspected to occur in these two species. As the next step in elucidating this mechanism, we genotyped with four highly variable microsatellite markers large numbers of eggs sampled from the fungus gardens of *Ac. echinatior* and *Ac. octospinosus* . Here we present the first estimate of the fraction of worker-derived eggs in queenright colonies of the two species, and we compare the results with the levels of worker reproduction predicted from ovarian dissections and from genotyping adult males.

19.7

THE EVOLUTION OF COOPERATION IN TERMITES

Judith Korb

University of Regensburg, Biology I, Universitaetsstr.30, D-93040 Regensburg, Germany

Cooperation is a fundamental characteristic of all major transitions in evolution by which new levels of selection evolved. By studying the transition from organisms to complex societies, social insects are good models to examine factors that promote the evolution of cooperation. However, so far research mainly concentrated on haplodiploid Hymenoptera while diploid Isoptera (termites) have largely been neglected. In the Australian drywood termite, *Cryptotermes secundus*, being a cooperative worker is no lifetime strategy but a condition dependent tactic. Individuals have a flexible development and can remain as cooperative workers in the nest or develop into selfish sexuals that found their own colonies. In field experiments, the influence of relatedness and ecological factors was examined for remaining as cooperative worker in the nest. A decrease or an increase in relatedness had no influence on the behaviour and development of termites. However, when food availability was reduced, individuals behaved more selfish and developed more often into dispersing sexuals. This can be ultimately explained by an increase in the costs and a decrease in the benefits of cooperative helping. In this species, food availability is linked to nest longevity as the termites nest in a piece of wood that they gradually consume and that they never leave to exploit new food sources. Thus, with declining food availability the nest longevity drops. This reduces the potential to gain indirect fitness by increasing the reproductives success of the colony. Furthermore, it increases the costs in direct fitness as the ratio between direct reproduction via dispersal to reproduction by inheritance of the natal breeding position increases. To conclude, these results suggest that low genetic variability within groups (colonies) is less important than the benefits of group living for cooperation in this termite.

Posters

19.8P

WORKER REPRODUCTION IN EUSOCIAL HYMENOPTERA

Robert L. Hammond, Laurent Keller

Institute of Ecology, Bâtiment de Biologie, Université de Lausanne, Lausanne CH-1015

Major evolutionary transitions require the evolution of mechanisms that moderate selfish interests by either nullifying or suppressing within group conflict. One such mechanism is mutual policing whereby members of a group collectively prevent individuals from acting in their own selfish interests. In social insects, kin selection theory predicts mutual policing behaviour by workers when workers are capable of laying male eggs and workers are collectively more closely related to queen-produced than to worker-produced male offspring. This is explicitly a relatedness-based theory and predicts that patterns of worker reproduction should be conditional upon the kin structure of the colony. We have collated published genetic data on patterns of male parentage, colony kin structure and on mean colony size for 51 species of eusocial insects. Using these data we have tested whether observed patterns of worker reproduction fit with predictions based upon relatedness and colony size using an independent contrasts approach.

19.9P

WORKER FERTILITY IN *FORMICA* ANTS: RELATEDNESS AND COLONY SIZE EFFECTS ON CONFLICT EXPRESSION

H. Helanterä, L. Sundström

University of Helsinki, PO BOX 65, FIN-00014 University of Helsinki, Finland

In social insect colonies a kin selected conflict over male production arises, since each female is most closely related to her own sons. Theory predicts that the workers are less fertile in colonies with high queen numbers since the worker majority should favour offspring of the queen. Workers are also predicted to be less fertile in large colonies because each worker is less valuable to the colony compared to the queen(s) as worker number increases. To study this we compared worker ovarian development and worker egg laying in queenless and queenright colony fragments in *Formica* ants with different queen numbers (range ca. 1 1000) and colony sizes (range ca. 1000 1 000 000). Our study species included the polygynous *F. fusca, F. transkaucasica, F. cinerea, F. polyctena* and *F. aquilonia* and the monogynous or slightly polygynous *F. rufa* and *F. pratensis*. In *F. exsecta* and *F. truncorum* both mono- and polygynous colonies were studied. Relatedness predictions were not met. Even highly polygynous species such as *F. cinerea, F. exsecta* and *F. truncorum* had high proportions of fertile workers (> 18%). Only the species where workers are very unlikely to encounter queenless conditions (*F. polyctena* and *F. aquilonia*) had clearly lower proportions of fertile workers (< 11%). Also in all other species queenless workers laid viable eggs, showing that fertile workers were not only trophic egg layers. Generally colony size was more important than kin structure as a determinant of conflict expression. Our results suggest that queen worker conflict over male parentage is expressed and workers try to impose their individual fitness interests even in large and polygynous societies and that both colony size and kin structure affect conflict expression. This shows that studies of kin structure should be combined to studies of factors determining benefits and costs of conflict behavior.

19.10P

DIPLOIDY, FACULTATIVE SEX AND THE MUTATIONAL LOAD

Szilvia Kover

Eotvos University, Pazmany P. s. 1/c, Budapest, Hungary

Diploids have higher mutational load than haploids, except for the case of sexual reproduction (with recombination) and truncation selection as former studies concluded. However, most probably at the beginning of the evolution of diploid sexual life-cycles meiosis did not contain recombination. My aim was to study the mutational load of this primitive syngamy-meiosis cycle without recombination and to compare its equilibrium mean fitness with that of haploid asexuality, endomitosis-meiosis cycle and normal sex with meiosis. I investigated different kinds of facultative sex in which the probability of sex depends on the number of mutations. I have found that sex decreased the diploid load even without recombination, but it was always higher than the haploid asexual load. The best type of facultative sex is where the individuals with zero mutation reproduce asexually and the rest sexually. It decreases the load even in case of multiplicative fitness function compared to diploid asexuality. I have also studied the chances of diploid strategies to spread in a population of haploid competitors and finally their resistance against Muller s ratchet. Complementation of partially recessive deleterious alleles give some transient advantage to various diploid systems that might have helped their spread. Even the primitive form of sex without recombination hinders Muller s ratchet.

19.11P

FITNESS EFFECTS OF BEGGING AND PROVISIONING, AND THE GENETIC COADAPTATION OF OFFSPRING AND PARENT

Judith E. Lock, Per T. Smiseth, Allen J. Moore

3.614 Stopford Building, School of Biological Sciences, University of Manchester, Oxford Road, Manchester M13 9PT

Extensive parental care is thought to have evolved because provisioning of food by parents to their offspring increases offspring fitness. Most research on parental care has been stimulated by, and stimulated, optimality approaches. These models make specific predictions regarding the evolution of optimal levels of signals and behavioural interactions between parents and offspring. Yet variation exists among parents in the quality of care that is provided. Genetic models of parental care help explain this variation and predict a genetic coadaptation between parental provisioning and offspring begging for food. We examine the fitness consequences of parental care in the burying beetle, *Nicrophorus vespilloides*, and tested for the predicted genetic coadaptation to explain variation in levels of care and begging that influence offspring fitness. We found that both begging and parental provisioning had positive effects on offspring life history characters. As predicted by genetic coadaptation models, the fitness of offspring cared for by unrelated individuals was different than the fitness of offspring cared for by their own mother. An examination of the level of care and the level of begging shown when individuals were cross-fostered demonstrated a positive genetic coadaptation between levels of care and levels of begging. Thus, in burying beetles a genetic coadaptation helps maintain variation in parental care and may speed the evolution of behaviour expressed in parent-offspring interactions.

19.12P

SELFISH MITOCHONDRIAL MUTANTS, GERM LINE BOTTLENECKS, AND PATERNAL LEAKAGE: A THREE LEVELS OF SELECTION MODEL

[1]D. Roze, [2]F. Rousset, [1]Y. Michalakis

[1]CEPM - IRD, 911 avenue Agropolis, BP 64501, 34394 Montpellier Cedex 5, France

[2]Institut des Sciences de l'Evolution, Université Montpellier 2, 34095 Montpellier Cedex, France

The population of mitochondrial DNA molecules of a species presents an inherent spatial structure, giving the opportunity for selection to act at multiple levels: between molecules within mitochondria, between mitochondria within cells, between cells within organisms, between organisms. Conflicts between levels of selection may arise in such situations, and indeed, examples of selfish mutants, which increase in frequency within the organism, but decrease the fitness of the organism, have been reported in yeast and humans. The spread of such mutants within populations depends on several factors influencing the relative effects of selection and drift at the different levels of organization. One of these factors is the presence of germ line bottlenecks: in many animal species, the number of mitochondria per cell is very low at some stage of the development of the germ line. By increasing the variance between cells, and decreasing the variance within cells, this bottleneck affects the relative strength of selection within and between cells. Another factor is the rate of paternal transmission of mitochondria. Until recently, the transmission of mitochondria was thought to be purely maternal in most species, a widely cited hypothesis to explain uniparental transmission being that it reduces the spread of selfish mutants. However, some evidence that paternal transmission occurs in humans has been reported recently. I will present a diffusion model to study the interplay between paternal transmission and germ line bottlenecks on the effect of selection against selfish mutants. I derive expressions for the probability of fixation of a single mutant, and for the mean equilibrium frequency of selfish mutants when mutation is recurrent. With tight bottlenecks, I find that paternal transmission increases the mean frequency of selfish mutants; I will present an explanation for this counter-intuitive result.

19.13P

PARTIAL BEGGING: AN EMPIRICAL MODEL FOR THE EARLY EVOLUTION OF OFFSPRING SIGNALLING

Per T. Smiseth, Allen J. Moore

University of Manchester, School of Biological Sciences, 3.614 Stopford Building, Oxford Road, Manchster M13 9PT, United Kingdom

The evolution of offspring begging is generally thought to be driven by conflicts of interest within families. In contrast to most previous studies, which have been conducted on birds or other species where the offspring only obtain food by begging from their parents, we focused on species where the offspring feed themselves in addition to begging for food from the parents. Such species, which can be described as 'partially begging', provide a unique empirical model for examining the origin and early evolution of offspring begging from non-signalling offspring foraging strategies. We used the partially begging burying beetle *Nicrophorus vespilloides* to test specific hypothesis concerning the coexistence of begging and self-feeding. We first tested the hypothesis that the cessation in larval begging coincided with an increase in efficiency of self-feeding. As predicted, begging ceased when the efficiency of self-feeding reached the point where the larvae grew just as well without as with access to food provided by the parent. We next tested whether the transition to nutritional independence occurred under parental or offspring control. The parent did not change its behaviour towards the larvae over time, while the larvae changed their behaviour by reducing the time spent begging in the presence of the parent. Food allocation during the transition to nutritional independence was therefore under offspring control. Our results suggest that there are low levels of behavioural conflict between parents and offspring during the transition to independence. We suggest more attention should be given to the significance of cooperative interactions among family-members.

19.14P

A GENE'S-EYE VIEW OF HORIZONTAL AND VERTICAL TRANSMISSION OF SYMBIONTS

Jeff Smith

Department of Biology, Emory University, Atlanta GA 30322, USA

The mode of symbiont transmission is widely hypothesized to play a major role in the evolution of parasitism and mutualism. Vertical transmission of symbionts from parent to offspring is thought to select for symbionts that are benign or beneficial, while horizontal transmission among unrelated individuals is thought to selected for those that are less beneficial or outright harmful. Selfish genetic elements seem to contradict these expectations, however, because they are able to spread and persist in populations despite having severe effects on their host's fitness and being passed exclusively from parent to offspring. Here I show that germline parasites are in fact consistent with virulence theory, provided that one take a gene's-eye view of horizontal and vertical transmission. In this view, vertical transmission is the association of host and symbiont genes across generations, while horizontal transmission is the colonization by symbionts of new genetic lineages. I show that, for selfish genetic elements, horizontal transmission is proportional to the amount of outbred sexual recombination and is required for the parasitic spread of both meiotic drive genes and cytoplasmic sex ratio distorters. In the latter case, increased vertical transmission caused by inbreeding or selfing favors female-biased sex allocation by nuclear genes, making the sex ratio distorter less parasitic. This theory allows transmission modes to be compared consistently across symbioses at different levels biological organization---whether they be between organisms, cells, or genes.

19.15P

FITNESS, LIFE-HISTORY, AND THE EVOLUTION OF COMPLEXITY IN VOLVOCALEAN GREEN ALGAE

Cristian A. Solari, Aurora M. Nedelc, Richard E. Michod

University of Arizona/ Department of Ecology and Evolutionary Biology, Biological Sciences West, Tucson, AZ 85721, USA

A model is developed to understand the transition from undifferentiated cell-groups to multicellular organisms with germ-soma separation, as a means to understand the emergence of individuality at a new higher level. We argue that the increase in complexity is a consequence of the trade-offs between the two basic fitness components fecundity and viability as size increases. We use volvocalean green algae to show that the evolution of increased complexity is driven by the resolution of these trade-offs. We compare the fitness, as size increases, of four hypothetical colony types with different degrees of germ-soma differentiation and show that soma evolves first, and, as size increases further, complete germ-soma specialization is achieved. Our results show that the cost of reproduction plays an important role in the evolution of multicellularity in Volvocales. Two general principles emerge from our work that may apply to other lineages: a cell group has to reach a specific number of cells to overcome the high cost of soma specialization, and soma, as the first specialization step, contributes to the integrity and individuality of the organism and increases viability, whereas germ, as the first specialization step, disrupts the integrity and individuality of the organism and decreases viability.

Symposium 20

The evolutionary roles of biased variation and internal selection

Organisers: Wallace Arthur & Alessandro Minelli

Roger Stevens Lecture Theatre 22

09.20 – 09.50	**Newman, S. A.** From physics to development: the evolution of morphogenetic mechanisms
09.50 – 10.20	**Stoltzfus, A.** Climbing Mount Probable: the mechanistic basis of orthogenesis
10.20 – 11.00	**Coffee**
11.20 – 11.20	**Fusco, G.** Interaction between selection and constraints in arthropod post-embryonic growth
11.20 – 11.40	**Chipman, A. D.** The gene and the egg – what is conserved and what is not in early arthropod embryogenesis
11.40 – 12.00	**Hansen, T. F.** The effect of epistatic gene interactions on evolvability
12.00 – 12. 20	**Azevedo, R. B. R.** Nematode cell lineages are computationally efficient
12.20 – 12.40	**General Discussion** Contributions from organisers, speakers and audience

12.40 – 14.00 Lunch

Invited talks

20.1

FROM PHYSICS TO DEVELOPMENT: THE EVOLUTION OF MORPHOGENETIC MECHANISMS

Stuart A. Newman

Department of Cell Biology and Anatomy, Basic Science Building, New York Medical College, Valhalla, NY, USA

Organismal forms have not always been generated by the highly integrated genetic programs characteristic of modern multicellular species. It is proposed that physical forces and other conditional processes played a more prominent role at earlier stages of evolution, establishing morphological templates that were consolidated by later genetic change. In particular, the most ancient multicellular creatures must have been simple cell aggregates that arose by adhesion of originally free-living cells, or by the failure of the same to separate after mitosis. Once this occurred, living organisms became susceptible to a set of physical determinants that were not relevant during the unicellular phase of evolution: diffusion over macroscopic distances, reaction-diffusion coupling, differential adhesion, and asynchrony between the cell cycle and periodic changes in cell-cell adhesion. These mechanisms, in turn, made inevitable developmental gradients, tissue multilayering, lumen formation and segmentation, and generated multifarious forms in organisms with identical, or marginally different, genomes. Subsequent stabilizing evolution, in this view, led to the hierarchical genetic circuitry characteristic of modern development. The idea that, with regard to the generation of three-dimensional form, the earliest multicellular organisms were more subject to physical determinants than are their modern counterparts, helps explain findings that are difficult to reconcile with the standard neo-Darwinian model. These include the burst of body plans in the early Cambrian, the punctuated character of morphological innovation, disparities between genetic and morphological evolution, and the conservation of developmental gene function in species separated by hundreds of millions of years of evolution.

20.2

CLIMBING MOUNT PROBABLE: THE MECHANISTIC BASIS OF ORTHOGENESIS

Arlin Stoltzfus

Center for Advanced Research in Biotechnology; 9600 Gudelsky Dr., Rockville, Maryland, USA

In the struggle to understand how development shapes evolutionary change, classical population genetics is of little help. While anyone might agree that the mechanics of development impose propensities on the process of variation, the notion that the trajectory of evolution reflects such propensities (orthogenesis) is a heresy in neo-Darwinism. According to the neo-Darwinian theory, the only role of variation is a negative one of imposing limits ("constraints") due to impossible variation; mutation and development cannot be evolutionary causes because they act at the "individual level"; propensities of variation cannot impose a direction on evolution because the stronger "force" of selection would oppose it. By means of a simple population-genetic model, I will show that each of these neo-Darwinian theoretical claims is invalid, and depends ultimately on the assumption that evolution can be equated with "shifting allele frequencies", as though "evolution" were merely the sorting out of pre-existing variation. When, instead, "evolution" requires a time-dependent process of the introduction of novel variants into a population (by events of mutation and altered development), biases in the introduction of variation become a directional or shaping force in evolution.

Contributed Talks

20.3

INTERACTION BETWEEN SELECTION AND CONSTRAINTS IN ARTHROPOD POST-EMBRYONIC GROWTH

Giuseppe Fusco

Department of Biology, University of Padova, via U. Bassi 58/B, I-35131, Padova, Italy

Natural selection and developmental constraints are continuously interacting processes in evolution. Although they have often been depicted as antagonistic forces of evolutionary change (a "positive" force the former, a "negative" force that resists the action of selection the latter), their complex interaction is not reducible to a simple opposition. This complex interaction can be fully appreciated in the evolution of arthropod post-embryonic development. In arthropods, metric growth occurs mainly in stepwise manner, post-embryonic development being paced by the moult cycle. Of several rules formulated for describing discrete size increment, Dyar's rule is considered a standard model for arthropod growth. Dyar's rule assumes a constancy of the postmoult/premoult size ratio between moults, and the linear size ratio, called Dyar's coefficient, is used in comparative studies. A growth progression conforming to Dyar's rule is a geometric progression. Several interpretations for Dyar's rule and for specific values of its coefficient have been offered so far, and these can be roughly split in two groups: selection-based and constraint-based explanations. The former suggests that a constant growth rate, possibly within a specific range of values, is promoted and actively maintained by natural selection. Examples are intra-specific competitive exclusion, food-finding strategy, growth strategy with respect to habitat stability, and maximization of growth efficiency. The latter considers a constant growth rates as the result of constraints set by growth physiology, like mechanism of intermoult hypodermal growth, and rates of cell proliferation. This investigation integrates data on arthropod metric growth with data on growth physiology and growth regulation. Dyar's rule and its possible adaptive values are considered in a broader context of ontogenetic size variation, that connects between-instars size increment to within-instar size variation. This specific case of study illustrates a general conceptual framework for confronting the roles of natural selection and developmental constraint in phenotypic evolution.

20.4

THE GENE AND THE EGG – WHAT IS CONSERVED AND WHAT IS NOT IN EARLY ARTHROPOD EMBRYOGENESIS

Ariel D. Chipman, Michael Akam

University Museum of Zoology, Downing St., Cambridge, UK

The developing embryo is subject to two major influences that determine its developmental patterns. The first is the reproductive ecology of the species, which determines the physical make up of the embryo – the shape and size of the egg, and the relative quantities of yolk. The second is the genetic history of the species, which determines which genes and genetic pathways are available for the construction of the embryo. It is the interplay of these two influences that defines the specific process of development for each species. We have compared the embryonic development and gene expression patterns in three species of arthropods: two insects, *Oncopeltus fasciatus* and *Thermobia domestica* and a centipede, *Strigamia maritima.* We focused on genes involved in the earliest stages of patterning, where the physical differences between embryos of different species are the most prominent. We looked at genes that define the embryonic A/P axis and at the gap genes, which define specific broad areas along that axis. Despite significant differences in the overall pattern of early stages of development, many of these genes are used in all three species at similar stages. Other genes diverge in their function and expression patterns and were presumably co-opted for different uses in different evolutionary lineages. A comparative analysis of embryonic gene expression together with a comparison of developmental pattern can help reconstruct how different ways of making an embryo have evolved.

20.5

THE EFFECT OF EPISTATIC GENE INTERACTIONS ON EVOLVABILITY

Thomas F. Hansen

Florida State University, Department of Biology, Tallahassee, FL 32306, USA

Evolvability, the ability to respond to a selection pressure, is often equated with the additive genetic variance of the trait, but epistatic gene interactions may modify even the short-term evolvability in at least three different ways: 1) By changing the additive genetic variance itself, 2) by building up favorable linkage disequilibrium, and 3) by directly modifying the response to selection. Over several generations, gene interactions may have large effects on evolvability. Mutational variance and directedness are also functions of the genetic architecture, and are evolvable whenever genes interact. This makes the dynamical evolution of gene interactions essential to understand evolvability on longer time scales. This contribution evaluates the effects of epistatic gene interactions on evolvability through analytical work and computer simulations.

20.6

NEMATODE CELL LINEAGES ARE COMPUTATIONALLY EFFICIENT

[1]**Ricardo B. R. Azevedo,** [2]Volker Braun, [3]Paul-Michael Agapow, [2]Hans-Peter Meinzer, [4]Armand M. Leroi

[1]*Dept. Biology & Biochemistry, University of Houston, Texas, USA*

[2]*Div. Medical & Biological Informatics, Deutsches Krebsforschungszentrum, Heidelberg, Germany*

[3]*Dept. Biology, University College London, London, UK*

[4]*Dept. Biology, Imperial College, Silwood Park, Ascot, UK*

What is the minimal amount of information required to specify the cells of a metazoan? Based on ideas from algorithmic information theory and phylogenetics, we have developed algorithms for inferring the minimum set of rules and determination events required to specify a cell lineage (Braun V, Azevedo RBR, Gumbel M, Agapow PM, Leroi AM, Meinzer HP. 2003. ALES: cell lineage analysis and mapping of developmental events. Bioinformatics, in press). Applying our algorithms to the complete embryonic lineage of the nematode *Caenorhabditis elegans*, we find that they are consistent with many known developmental events required to specify cell fates.

We then show that fewer rules and determination events are required to specify the actual *C. elegans* lineage than lineages simulated under null models. Furthermore, some cell fates (e.g., intestinal, body muscle) appear to be more efficiently specified than others (e.g., neuronal, programmed cell death). A similar pattern is observed in another species of nematode, *Pelliodites marina*, despite extensive interspecific differences in lineage topology and cell fate assignments relative to *C. elegans*. We propose that selection for increased computational efficiency is a major force in molding the evolution of nematode embryonic cell lineages.

Posters

20.7P

ISOLATION, CHARACTERIZATION, CHROMOSOMAL MAPPING AND COPY NUMBER OF A TANDEMLY REPEATED CLUSTER OF FIVE HISTONE GENES IN THE MUSSEL *MYTILUS GALLOPROVINCIALIS*

[1]J. M. Eirín-López, **[2]A. M. González-Tizón,** [1]A. Martínez, [2]M. .F. Ruiz, [2]L. Sánchez, [1]J. Méndez

[1]*University of A Coruña, Dpt. Biología Celular y Molecular, Campus de A Zapateira s/n, E15071 A Coruña, Spain*

[2]*Centro de Investigaciones Biológicas, Velázquez 144, E28008 Madrid, Spain*

Histones are a group of small basic nuclear proteins involved in the organization and function of the eukaryotic chromatin. The characterization of these genes in a great variety of organisms has shown a high degree of heterogeneity regarding to their organization, structure, and expression patterns. The characterization of the remaining histone genes (H2A, H2B, H3, H4) into the repetitive unit is persuaded in the present work. A genomic library of the mussel *Mytilus galloprovincialis* was screened in order to isolate and characterize the histone repetitive unit, being defined as H4-H2B-H2A-H3-H1, followed by two 5S rRNA genes. Typical promoter elements were identified at 5′ regions, and also additionally orphan features were presented by H1 promoter regions. The number of histone gene copies was estimated by dot-blot as 198-222 copies per haploid genome for H2A-H2B genes, and as 210-223 copies per haploid genome for H3-H4 genes. The chromosomal location of these genes were determined on *M. galloprovincialis* chromosomes by FISH, with a 4.2 Kbp probe in which the four core histone genes are included. Two pairs of signals in two different chromosome pairs were evidenced and one of them, located at telomeric positions, is likely to group the big majority of the genes given its high signal intensity. The results obtained allow us to confirm the presence of "orphan" H1 genes independently organized, and in a different chromosome, from the H1 genes in the repetitive units. Also, the presence of two different mRNA termination signals have very important implications regarding to the evolution of expression patterns dependent or independent from the S phase of the cell cycle. This work was supported by a PGIDT grant awarded to Dr. J Méndez (10PX110304PR).

Symposium 21

Evolution on islands - patterns of colonisation, adaptation and speciation

Organisers: Sara Goodacre & Angus Davison

Conference Auditorium 1

14.00 – 14.30	**Gillespie, R. G.** Evolution of spiders on Oceanic islands: the venture of few and gain of many
14.30 – 15.00	**Meyer, A.** Patterns and processes of colonization and radiation in East African cichlid fish species flocks
15.00 – 15.20	**Roderick, G. K.** Colonisation of the insular Pacific by herbivorous insects: the role of host shifts and dispersal
15.20 – 16.00	**Tea**
16.00 – 16.20	**Clegg, S. M.** Microevolution in an island bird group, the silvereyes of the southwest Pacific
16.20 – 16.40	**Leys, R.** Islands in the desert: Evolution of subterranean water beetles in arid Australia
16.40 – 17.00	**Adamowicz, S. J.** Intercontinental phylogeography and the radiation of *Daphnia*
17.00 – 17.20	**Jordal, B. H.** Distinguishing insular isolation from host switching in the diversification of Macaronesian beetles breeding in *Euphorbia* spurges

Invited talks

21.1

EVOLUTION OF SPIDERS ON OCEANIC ISLANDS: THE VENTURE OF FEW AND GAIN OF MANY.

Rosemary G. Gillespie

Insect Biology, 201 Wellman Hall, University of California, Berkeley, CA 94720-3112

Adaptive radiation involves the diversification of species to exploit different ecological roles, with related adaptations. It is often associated with colonization of new environments that are sufficiently isolated as to allow populations to diversify by filling multiple ecological roles. How is the diversification achieved? I have been studying spiders in the genus *Tetragnatha* to elucidate commonalities underlying patterns of adaptive radiation. Here, I first compare three archipelagoes of differing isolation across the Pacific and show that the genus has undergone adaptive radiation within each archipelago, although the lineages within each are only distantly related. Second, I compare different lineages within the Hawaiian Islands, where diversification is the most prolific, to determine how species differentiation occurs within the archipelago. The temporal framework of the islands allows examination of the changing pattern of adaptive radiation over time, as lineages have generally progressed down the island chain from older to younger islands. Ecological disparity among taxa is highest on one of the youngest islands, suggesting that diversification may be largely confined to the short period immediately following island formation. In addition, species in the spiny-leg clade on any one island are most closely related to others on the same island, and the same set of ecological forms has evolved repeatedly on different islands. Together these results suggest that adaptive radiation is characterized by rapid and episodic, ecologically-driven diversification of species.

21.2

PATTERNS AND PROCESSES OF COLONIZATION AND RADIATION IN EAST AFRICAN CICHLID FISH SPECIES FLOCKS

Axel Meyer

Department of Biology, University of Konstanz, Universitätsstr. 10D-78457 Konstanz, Germany

The large lakes in East Africa each contain a species flock composed of hundreds of species of cichlid fishes. The adaptive radiations of cichlid fishes are characterized by their extremely fast rates of speciation and their high diversity in terms of species and morphological variation. Based on studies of mitochondrial and nuclear DNA markers we have increased our understanding of the patterns of relationships and the ages of particular lineages of cichlids. With mitochondrial and microsatellite maker based studies we have inferred processes of diversification and find that in many places in the lakes similar phenotypes evolved independently. In a recent mitochondrial-DNA based study we find that the radiation of cichlids of the Lake Victoria superflock is diphyletic and derived from Lake Kivu cichlids. We estimate the the Lake Victoria superflock is about 100,000 years old. I will present a scenario of the colonization history of Lake Victoria in a phylogeographic context of Eastern Africa.

Contributed talks

21.3

COLONISATION OF THE INSULAR PACIFIC BY HERBIVOROUS INSECTS: THE ROLE OF HOST SHIFTS AND DISPERSAL

George K. Roderick,

University of California, Insect Biology, 201 Wellman Hall, Berkeley, California, USA

Abstract Text: The factors that lead to adaptive radiation are currently receiving much attention, particularly the role of habitat specialization and a reduction in dispersal ability (for reviews of these issues for island arthropods, see Roderick & Gillespie 1998, Molecular Ecology; Gillespie & Roderick, Ann. Rev. Entomology 2002). Here, I use plant-feeding insects to examine (1) the association between colonisation of new habitats and host-shifts and (2) whether reduced dispersal ability is important for host-shifts and subsequent adaptive radiation. Planthoppers in the genus *Nesosydne* (Hemiptera: Delphacidae) are one of the most specious groups of planthoppers and are found only in the Insular Pacific, particularly Hawaii, the Marquesas, the Societies, the Australs as well as the Galapagos. In Hawaii, the group numbers over 80 described species. Unlike their continental counterparts that are highly specialized monocot (grass, sedge) feeders, species in the Pacific have switched onto numerous plant species in many plant families, and primarily dicots. For example, the *Nesosydne* species in Hawaii feed on plants in over 27 different families. However, like their continental counterparts, the species in the Pacific remain extremely specialized, feeding usually on only one host species. Oviposition and development are also closely tied to the host as is mate-finding through plant borne auditory signals. A phylogenetic analysis shows that although there is some historical constraint in the types of plant hosts that are used, island colonisation is often associated with host-shifting. Many species of planthoppers in the Pacific show a reduction in flight ability as expressed by having reduced wings as adults. However, there is little evidence to tie this reduction in dispersal to rates of adaptive radiation in the group

21.4

MICROEVOLUTION IN AN ISLAND BIRD GROUP, THE SILVEREYES OF THE SOUTHWEST PACIFIC

[1]**S. M Clegg**, [1]I. P. F Owens, [2]S.Scott, [3]A. Estoup,

[1]*Imperial College London, Dept Biological Sciences, Silwood Park, Ascot, UK*

[2]*University of Queensland, Dept Zoology and Entomology, St Lucia, Australia*

[3]*Campus International de Baillarguet, Centre de Biologie et de Gestion des Populations, Montferrier, France*

There are a number of factors that potentially influence the differentiation of island forms following colonization. These include aspects of the colonization process itself, such as effective founder population size, the effects of geographical isolation and the pressures of a novel selective environment. In the southwest Pacific, members of the Zosteropidae family have repeatedly colonised islands and have subsequently differentiated to varying extents. Here we examine the processes that may have contributed to morphological differentiation in island *Zosterops* forms of different ages. We combine information on neutral molecular data and morphology to examine the potential roles of drift and selection in differentiation of these forms. Patterns of molecular variation in recently colonized populations suggest that the founding of a new population is not generally accompanied by significant molecular shifts, and Bayesian models suggest that this is because effective founder flock sizes were relatively large. Additionally, both patterns and rates of morphological differentiation suggest that selective mechanisms play an important role in differentiation, specifically a trend towards large body size. We discuss the role of one potential selective mechanism that may drive large body size; that of a shift towards generalist foraging behaviour in insular conditions of decreased interspecific competition. Larger body size in island birds has been proposed to facilitate generalism, and therefore could offer a selective advantage.

21.5

ISLANDS IN THE DESERT: EVOLUTION OF SUBTERRANEAN WATER BEETLES IN ARID AUSTRALIA

[1]**Remko Leys**, [1]Steve J. B. Cooper, [1]Chris H. S. Watts, [2]William F. Humphreys,

[1]*South Australian Museum, Evolutionary Biology Unit, North Terrace, SA 5000, Adelaide, Australia*

[2]*Western Australian Museum, Francis Street, WA 6000, Perth, Australia*

The subterranean calcrete aquifers of arid inland Australia constitute an archipelago of more than 200 isolated 'islands'. These aquifers have recently been found to contain a surprisingly rich invertebrate subterranean water fauna (stygofauna), comprising Amphipoda, Syncarida, Ostracoda, Copepoda and also the world's most diverse assemblage of subterranean diving beetles (Coleoptera: Dytiscidae). A total of 17 % of the aquifers (n = 36) have now been sampled, which yielded assemblages of two to five unique species of water beetles per aquifer. In this study we investigate the evolutionary origin of this beetle fauna by linking species divergence times to geological and palaeoclimatic data. We constructed a phylogeny based on two sequenced fragments of mitochondrial genes (CO1 and 16S-tRNA-ND1). To estimate divergence times, the phylogeny was linearized using a relaxed molecular clock method. We found that, 1) assemblages within an aquifer consist of distantly related lineages and/or a single pair of sister species that differ significantly in size and morphology, 2) evolutionary transitions from surface to subterranean life took place within a relatively small time frame between 9 and 4 Mya (million years ago), and 3) most of the variation in divergence times of the sympatric sister species is explained by the variation in latitude of the localities, which correlates with the onset of aridity from the North to the South and with an aridity maximum in the Early Pliocene (5 Mya). We conclude that individual calcrete aquifers were colonized by a number of distantly related diving beetle lineages. Several lines of evidence from molecular clock analyses indicate a causal link between the evolutionary transitions to subterranean life and the aridification during the Late Miocene and Early Pliocene.

21.6

INTERCONTINENTAL PHYLOGEOGRAPHY AND THE RADIATION OF *DAPHNIA*

[1]**Sarah J. Adamowicz,** [2]Paul D. N. Hebert, [3]John K Colbourne, [1]Andy Purvis,

[1]*Imperial College London, Silwood Park, Ascot, SL5 7PY, UK*

[2]*University of Guelph, Guelph, Ontario, N1G 2W1, Canada*

[3]*Indiana University, Bloomington, Indiana, 47405-3700, USA*

The study of evolution in inland waters provides an excellent complement to the larger body of work on terrestrial-island biota. Together, these studies provide a more complete understanding of the role of isolation in the evolution of diversity. We present here the results of a polycontinental investigation of the evolutionary radiation of the species-rich genus *Daphnia*, a dominant microcrustacean of inland-water islands. Members of this genus have been important model organisms for studies on metapopulation structure as well as analyses of allopatric and ecological divergence. The large geographic scope of this study provides new insights into processes operating at multiple temporal and geographic scales. Through a phylogenetic analysis of more than one hundred species from four continents, we assess the relative roles of long-range dispersal, regional genetic structure, ancient vicariance events, and ecological shifts in the diversification of daphniids. Our results indicate that ecology, geography, and historical contingency combine in fascinating ways to structure contemporary patterns of diversity. In addition, we use comparative analyses to identify key factors associated with elevated rates of cladogenesis in some lineages. Finally, we compare these patterns of diversification with those in other well-studied insular taxa.

21.7

DISTINGUISHING INSULAR ISOLATION FROM HOST SWITCHING IN THE DIVERSIFICATION OF MACARONESIAN BEETLES BREEDING IN *EUPHORBIA* SPURGES.

Bjarte H. Jordal, Godfrey M. Hewitt,

University of East Anglia, School of Biological Sciences, Norwich NR47TJ, UK

Insect-plant associations and island archipelagos have independently provided much insight to the process of adaptation and diversification. In this study, we explore the relative importance of islands and host plants as isolating mechanisms in the diversification of a group of bark beetles feeding and breeding in woody *Euphorbia* spurges. All species in the genus *Aphanarthrum* are each associated with only one species group of *Euphorbia* (succulents or three different arborescent groups). Furthermore, the majority of species are endemic to one or several of the Macaronesian Islands, with the remaining species restricted to Africa. Hence, putative mechanisms of speciation could be assessed by identifying pairs of sister species in a phylogenetic analysis. We used DNA sequences from two mitochondrial and two nuclear genes, and 28 morphological characters, to reconstruct the genealogical relationships among 92 individuals of 30 species and subspecies of *Aphanarthrum* and related outgroup genera. An arborescent breeding West-African species was consistently the most basal taxon in *Aphanarthrum*. Two major radiations followed, one predominantly African lineage of succulent feeding species, and one predominantly island radiation associated with arborescent host plants. Few cladogenetic events were associated with host switching alone, leaving other isolating factors more important in the diversification process. Sister comparisons showed that the most recent divergences occurred in allopatry on closely related hosts, with subsequent expansions obscuring the more ancient events. However, more detailed genetic studies were performed to assess the areas of origin for currently widespread, co-existing, and ecologically similar species, showing that at least some of these species originated on different islands. We further show that speciation is an ongoing process on some of the younger islands, with nuclear genes reflecting this process more clearly than mitochondrial genes.

Posters

21.8P

GEOGRAPHIC VARIATION IN PITVIPER VENOM : NATURAL SELECTION, OR NEUTRAL EVOLUTION?

S. Creer

School of Biological Sciences, University of Wales - Bangor

Intraspecific variation in snake venom composition has wide ranging implications for fields ranging from snakebite management to the identification of biological resources for research and therapy. This study aimed to elucidate the underlying mechanisms of venom evolution using *Trimeresurus stejnegeri* in Taiwan and Pacific insular populations ($n<229$) as a model system. Matrix correspondence tests and independent contrasts were used to measure associations between venom composition (measured by electrophoretic and mass spectrometric analyses) against phylogenetic (mtDNA analyses) and ecological (diet composition) correlates in a spatial framework. Geographic variation in venom composition was primarily between Taiwan and two Pacific islets. Despite the common assumption that venom variation is a product of neutral molecular evolution, statistical testing failed to convincingly link venom variation with phylogenetic descent. Instead, pronounced differences in venom composition may be the product of natural selection for regional diets, or of independent founder effects.

21.9P

ECOLOGICAL SELECTION AND SPECIATION OF *MANDARINA* LAND SNAILS ON THE OCEANIC OGASAWARA ISLANDS

[1]Angus Davison, [2]Satoshi Chiba,

[1]ICAPB, Ashworth Laboratories, West Mains Road, University of Edinburgh, Edinburgh, EH9 3JT, UK

[2]Division of Ecology and Evolutionary Biology, Graduate School of Life Sciences, Tohoku University, Aramaki-Aza-Aoba, Aoba-ku, Sendai 980 8578, Japan

The Ogasawara Islands are about 30 small volcanic islands in the north-west Pacific, about 1000 km south of Japan. The endemic land snail genus of these islands *Mandarina* shows exceptionally rapid evolution of morphological and ecological traits, in addition to high DNA diversity. Previous work has shown that sequential adaptive radiations occurred on different islands, so that species with similar morphologies and life habits appeared repeatedly and independently in different lineages and islands at different times. Shell morphology is closely related to life history, so that arboreal, semi-arboreal and ground-living forms come to resemble snails on different islands from different lineages. We have been studying speciation in this genus, in particular using a combination of ecological techniques and lab-based genetic methods to gauge the potential for sympatric speciation. A preliminary analysis of the results will be presented concentrating on individuals of a ground-living form which compete for a continuously distributed resource, the variety of leaves and leaf-litter that is their diet, and the different strategies that may be used to avoid predation, dessication or heat-stress. The resulting disruptive selection may have repeatedly produced two forms on different islands, which differ in their shell shape, behaviour, migration ability, diet and DNA.

21.10P

DNA-BASED PHYLOGENY OF THE HONEY-BUZZARDS (GENUS *PERNIS*)

Anita Gamauf, Elisabeth Haring

Museum of Natural History Vienna, 1. Zool Dept., Burgring 7, A-1014 Vienna, Austria

To investigate geographical differentiation and speciation of the Honey-buzzards a molecular phylogeny was established using a partial sequence of the cytb gene (382 bp). We analysed 35 specimens of the genus Pernis representing all valid taxa (10) and representatives of the Old World Perninae, namely Long-tailed Honey-buzzards Henicopernis and Cuckoo-hawks Aviceda, to assess their relationship to the genus Pernis. This molecular phylogeny can be considered as a first approach for inferring the phylogenetic relationships of Pernis and related genera and for addressing questions concerning their evolutionary history, biogeography and systematics. The presumed relatives Bearded Vulture Gypaetus barbatusand Egyptian Vulture Neophron percnopterus as well as the Common Buzzard Buteo buteo were used as outgroup taxa. In the trees derived from the sequence data Aviceda appears as the basal lineage of the genus Pernis, whereas the genera Pernis, Henicopernis, and the Old World vultures Gypaetus and Neophron are not closely related. Species status of P. apivorus and P. ptilorhyncus are confirmed. The relationships of the two clades representing three subspecies of P. celebensis are not clearly resolved. We propose to split this taxon into the species P. celebensis (Sulawesi) and P. steerei (Philippines).

21.11P

ENHANCED COLOUR POLYMORPHISMS IN ISLAND LAND SNAILS

M. Hayashi, S. Chiba

Graduate School of Life Science, Tohoku University, Aobayama, Sendai, Japan

Variations in visible genetic polymorphisms are assumed to decrease in populations of small islands due to intense founder effects, genetic drift and inbreeding. However, we have found evidence of a marked enhancement of colour polymorphisms within populations in small oceanic islands that were colonized from the mainland. The source populations on the mainland of the land snail *Euhadra peliomphala* in four oceanic islands were estimated by phylogenetic analysis of mitochondrial DNA sequences. Diversity of shell colour was higher in the island populations than in the source populations on the mainland. In addition, the shell colour morphs differed not only among populations from different islands but also between the island populations and the source populations on the mainland. In contrast, no mtDNA variations were found in any of the island populations on the main land. In contrast, no mtDNA variations were found in any of the island populations, even though the source populations possessed high mtDNA diversity. Thus, novel colour morphs appeared in the island populations after their colonization, and colour polymorphisms are enhanced in these islands despite the loss of genetic variation. The above findings suggest that ecological mechanisms such as morphological release due to a release from competition and predation overcome the tendency toward reduced genetic variation in islands to enhance the colour polymorphism.

21.12P

THE ORIGIN AND EVOLUTION OF SMALL MAMMALS ON THE WESTERN AND NORTHERN ISLES OF SCOTLAND

Jeremy S. Herman

University of York, Department of Biology, York YO10 5YW, UK

The distributions of small mammals on the Hebridean, Orkney and Shetland islands reflect their postglacial and human-mediated colonisation from sources in mainland Britain or Europe. Considerable effort has been made by previous workers to describe the well-marked phenotypic variation in these animals and to relate it to their distributions among the islands, but the origins and relationships of these populations mostly remain in doubt. Molecular phylogenies, based on DNA sequences, are now established as a means to infer colonisation history of small mammals. Maternally inherited mitochondrial and paternally inherited Y-chromosome sequences are of particular use and both are employed here to establish the colonisation history of these islands by small mammals and to consider the processes involved in their differentiation. Comparisons will be made with phenotypic data from geometric morphometric methods and with non-metrical skull variation, to test the value of these characters in inferring colonisation history.

21.13P

A SOUTHERN AFRICAN RIVERINE CICHLID PHYLOGENY: HOW DOES IT COMPARE WITH THE RADIATIONS IN THE GREAT LAKES?

[1]D. A. Joyce, [1]D. H. Lunt, [2]R. Bills, [3]M. E. Knight, [1]G. F. Turner, [1]O. Seehausen

[1]*School of Biological Sciences, The University of Hull, Hull HU6 7RX, UK*

[2]*South African Institute for Aquatic Biodiversity, Somerset St, Private Bag 1015, Grahamstown 6140, South Africa*

[3]*School of Biological Sciences, The University of Southampton, Bassett Crescent East, Southampton SO16 7PX, UK*

The haplochromine cichlid flocks of the African Great Lakes are perhaps the best examples of rapid and extensive speciation known, with the largest recent radiations occurring in Lakes Victoria and Malawi. Haplochromine cichlids also occur in rivers and smaller lakes, and insight into the radiation of the Great Lakes faunas may be gained from comparative study with these less species-rich groups. We investigated the radiation of a previously understudied group of cichlids from southern Africa. The purpose of the study presented here is two-fold. Firstly, to investigate the diversity found in the southern African riverine cichlids in an attempt to compare a riverine radiation to the lake radiations. Secondly, to investigate the relationship between this large group of riverine species and the lake radiations.

21.14P

PARASITES & IMMUNITY OF DARWIN'S FINCHES ON ISLANDS

K. Lindstrom

Dep. of Biol. and Environ. Science, University of Jyvaskyla, P.O. Box 35, FIN-40014 University of Jyvaskyla, FINLAND

The absence of parasites in the environment can relax selection for parasite resistance. In this study we have examined whether immune responsiveness differs between populations of birds along a gradient of parasite-mediated selection. Island biogeography models predict that the number of species per area, both hosts and pathogens, should be higher on larger islands. Furthermore, epidemiological models predict parasite prevalence to be higher in larger populations. We measured parasite prevalence and load in relation to immunity in small ground finches in four island populations in the Galapagos archipelago. Parasite prevalences and loads where higher on larger islands, for a sample of three types of infections. When challenged with a novel antigen, birds on larger islands mounted weaker cell-mediated immune responses. In contrast, birds on larger islands had higher baseline levels of antibodies. In combination these data suggest that animals living in parasite-rich communities down-regulate cellular immunity to avoid costs associated with immune responses but rely to a higher extent on cross-immunity for protection. Comparative studies in island ecosystems can provide a valuable insight in how animals maintain natural immunity to pathogens.

21.15P

THE PHYLOGENY OF THE EAST AFRICAN HAPLOCHROMINE CICHLIDS

Tanja Mack, Walter Salzburger, Axel Meyer

Department of Biology, University Konstanz, Universitaetsstrasse 10, 78457 Konstanz, Germany

The East African lakes and river systems harbor an extremely diverse cichlid fish fauna of almost 3.000 species. Many researchers have studied the cichlid communities - especially the endemic species flocks of lakes Victoria, Malawi and Tanganyika - as model systems for evolutionary processes. With a total of 1,700 species, the haplochromine cichlids form the most species-rich assemblage, and it has traditionally been assumed that riverine haplochromines seeded the species flocks in all large lakes in the East African Rift valley. More recently, it has been proposed that the Haplochromini form a polyphyletic assemblage, and that the majority of species share an ancestor with the mouth-brooding Tropheini from Lake Tanganyika. Here we present a phylogeny of the East African haplochromine cichlids including all major riverine and lacustrine lineages. Our analyses of two mitochondrial gene segments (898 bp of the control region, 1047 bp of the NADH Dehydrogenase Subunit 2 gene) are based on more than 200 specimens, thus providing the most comprehensive phylogenetic hypothesis so far. We confirm the paraphyly of the Haplochromini and the placement of members of the *Orthochromis/Schwetzochromis* species complex outside the remaining taxa. We also show that several haplochromine lineages independently migrated from Lake Tanganyika into surrounding river systems and further on to other Rift Valley lakes.

21.16P

CHROMOSOMAL AND ECOLOGICAL CHARACTERISATION OF TWO PARAPATRIC RACES OF THE HOUSE MOUSE SHARING A CONTACT ZONE IN THE ISLAND OF MADEIRA (PORTUGAL)

[1]A.C. Nunes, [2]J. Britton-Davidian, [3]M.G. Ramalhinho, [2]J. Catalan, [4]R.Capela, [1]M.L Mathias, [2]G. Ganem

[1]Universidade de Lisboa, Centro de Biologia Ambiental, Departamento de Biologia Animal, C2 3° Piso Campo Grande, 1749-016 Lisboa, Portugal

[2]Université Montpellier II, Laboratoire de Génétique et Environnement, Institut des Sciences de L' Evolution, PI. E. Bataillon CC065, 34095 Montpellier 05, France

[3]Universidade de Lisboa, Centro de Biologia Ambiental, Museu Bocage, Rua da Escola Politécnica, 1200 Lisboa, Portugal

[4]Universidade da Madeira, Departamento de Biologia, Penteada, 9000 Funchal, Portugal

Six chromosomal races of the house mouse were described in the island of Madeira where mice, although commensal, are mainly outdoors. This island is characterised by sharp altitudinal and climatic gradients. Although most races are separated by geographical barriers, two are parapatric and share a contact zone. Several factors could be involved in the dynamics and evolution of the contact zone: 1) Adaptation to differing ecological conditions which could limit gene flow through the contact zone; 2) Chromosomal incompatibilities leading to partially fertile hybrids and a postzygotic barrier to gene flow; 3); Premating divergence between races leading either to their isolation or asymmetric introgression; 4) The absence of the three above resulting in an expansion of the contact zone and chromosomal polymorphism. The first hypothesis was investigated by sampling mice at 3 Km intervals along a 39-Km transect in the south-western part of the island (32 sites, 555 mice). Mice were karyotyped and the following ecological parameters of trapping sites were recorded: altitude, temperature and type of vegetation. An additional parameter concerned macrohabitat variables related to human dispersion and activities, as they may have a bearing on dispersal of mice. The two races share 7 metacentric fusions, and differ by the additional presence of Rb(6.7) in one race and Rb(7.15) in the other. Hybrids between the two races, although viable, are expected to suffer from infertility. Results of the chromosomal analysis showed i) the presence of only 2 hybrids, ii) a gradual decrease in frequency of Rb(6.7) and Rb(7.15) towards the contact zone, and iii) a preponderance of individuals carrying neither of these fusions in the center of the contact zone. Variation of the ecological parameters through the transect and its relationship to that of chromosomes is discussed.

21.17P

ADAPTATION TO SERPENTINE SOILS: EVOLUTION OF SITE-SPECIFIC ECOTYPES IN *CERASTIUM ALPINUM*

[1]A.- B. Nyberg Berglund, [2]A. Westerbergh,

[1]Department of Natural and Environmental Sciences, Mid Sweden University, SE-851 70 Sundsvall, Sweden

[2]Department of Plant Biology and Forest Genetics, Swedish Agricultural University, SE-750 07 Uppsala, Sweden

The alpine plants in Scandinavia are pioneers that invaded the areas exposed by the melting ice sheet at the end of the last Ice Age. Forests advanced rapidly and the alpine plants now grow within relatively restricted areas in the mountains. Some alpine plants have, however, persisted within the boreal forests on isolated serpentine islands. Serpentine soils are rich in Ni and Mg and have a distinct flora. We study the evolution of serpentine tolerance in the alpine pioneer plant *Cerastium alpinum* (Caryophyllaceae). Enzymatic studies of *C. alpinum* suggest that the postglacial immigration involved two independent colonization events, one from the east and one from the west. The two lineages that differ genetically seem to come into contact in a hybrid zone in northern Scandinavia. We have compared the effects of Ni and Mg on the growth of plants from serpentine and adjacent non-serpentine populations in the west, east and the proposed hybrid zone. Seedlings were placed in solutions with either high or low levels of Ni and Mg in a full factorial experiment arranged according to a randomized block design. The serpentine populations showed higher tolerance to Ni and Mg stress than non-serpentine populations. However, the degree of tolerance differed among the serpentine populations and the mode of tolerance for a serpentine population seems to be related to the specific characteristics of the soil of that population. These results suggest that the *C. alpinum* plants in the two immigrating populations differed in the response to metal stress rather than that the populations were constitutively adapted to serpentine. Site-specific serpentine ecotypes have evolved during the postglacial colonization of Scandinavia.

21.18P

REGIONAL PERSISTENCE IN A PATCHY AND LOCALLY UNSTABLE WORLD

[1]Gisep Rauch, [2]Wolfgang W. Weisser,

[1]Max Planck Institute of Limnology, August-Thienemann-Str. 2, 24306 Plön, Germany

[2]Institute of Ecology, University of Jena, Dornburger-Str. 159, 07743 Jena, Germany

Dispersal rate is a key factor for predator-prey and host-parasitoid metapopulations, allowing regional persistence despite frequent local population extinctions. Host-parasitoid interactions with a high degree of resource specialisation are excellent model systems to test assumptions of metapopulation theory in the field, because dispersal rate can be manipulated by increasing the distance between local populations. In a field experiment we tested the influence of dispersal rate on regional persistence of *Lysiphlebus hirticornis*, a specialist parasitoid of the monophagous aphid *Metopeurum fuscoviride*. Regional persistence of the parasitoid was measured as the time it survived in a host population group. A host population group consisted of local aphid populations on seven tansy plants. The parasitoid was released on the central plant. Four distance treatments were established where the distances between the plants were either one, four, 16 or 64 metres. Dispersal rate and regional persistence of parasitoids decreased with increasing distance between local aphid populations.

21.19P

HOW TO FIND SPECIES AMONG ALL THE GENES: GENE-SPECIES TREE CONFLICT IN A RADIATION OF VIVIPAROUS FRESHWATER GASTROPODS (CERITHIOIDEA: PACHYCHILIDAE) IN THE ANCIENT LAKES OF SULAWESI, INDONESIA

Thomas von Rintelen, Matthias Glaubrecht

Institute of Systematic Zoology, Museum of Natural History, Invalidenstr. 43, 10115 Berlin, Germany

Species flocks of viviparous freshwater gastropods in two separate ancient lake systems on Sulawesi, viz. Lake Poso and the five lakes of the Malili system, have been used as model systems to study speciation in long-lasting lacustrine environments. A mtDNA based molecular phylogeny has shown the existence of independent radiations in the two lake systems, with one and three well-defined molecular clades in Lake Poso and the Malili system, respectively, suggesting several colonization events. A comparison of molecular and morphological data within the individual clades, i.e. at the species level, has revealed an almost complete mismatch. Possible explanations for this phenomenon include incomplete lineage sorting, the existence of cryptic species, a "lumping" attitude in previous species recognition, or hybridization. However, the evident gene-species tree conflict is reflected in equally incongruent distributions of key species-defining morphological characters such as the shell and radula. In addition, a less conspicuous molecules-morphology mismatch is found at the clade level. Considering all evidence, we regard hybridization as the most likely process responsible for the observed pattern. As at least some of the radula (and thus trophic) polymorphism observed can be linked to differences in habitat, hybridization might promote diversification or even speciation.

21.20P

POPULATION STRUCTURE AND DEFINITION OF MANAGEMENT UNITS OF THE INSULAR ENDEMIC AZOREAN BAT (*NYCTALUS AZOREUM*)

P. Salguerio

Universidade de Lisboa

The Azores archipelago is located in the North Atlantic about 1500 Km distant from mainland Portugal and comprises nine major islands. Due to its remoteness, few terrestrial vertebrates colonised successfully this archipelago. One exception is the Azorean bat (*Nyctalus azoreum*), which is the only endemic mammal from the Azores, present in most of the islands. *N. azoreum* is thought to have evolved from a continental ancestor related to the Leisler's bat *Nyctalus leisleri*, however not much is known about its ecological needs and population genetic variability. Our aim was to study the gene diversity and population structure of this vulnerable species. Mitochondrial *D*-loop was sequenced in 159 bats from 14 colonies distributed on six islands. Fifteen haplotypes were detected, six of which were unique to one island still, one was found all over the archipelago. Nucleotide diversity was low, possibly due to the original founder effect. Genetic diversity was strongly concordant with geographic distance. Hence, populations among islands were highly structured. This pattern of mtDNA variation suggested moderate gene flow among islands of the Central group but, very limited gene exchange between this group and the island of S. Miguel. Therefore, these two units should be managed separately in order to preserve the unique attributes of the Azorean bat.

21.21P

INTERACTIONS BETWEEN THE HOST PLANT *FILIPENDULA ULMARIA* AND ITS NATURAL ENEMIES IN AN ARCHIPELAGO

Johan Stenberg, Lars Ericson,

Dept. Ecology and Environmental Science, Umeå University, SE-90187 Umeå, Sweden

The aim of our work is to understand the direction and strength of the interactions between the host plant *Filipendula ulmaria* and its natural enemies, in an archipelago affected by isostatic rebound. Depending upon host population size and age, and location in the archipelago, host populations are gradually colonized by different natural enemies; the two most important being the rust fungus *Triphragmium ulmariae* in the middle part of the archipelago, causing host mortality, and the chrysomelid beetle *Altica engstroemi* in the inner part of the archipelago, causing host defoliation. We study the strength and direction of these interactions in relation to earlier disease history. We report data for *Altica engstroemi* showing that it discriminates between host populations and that (1) earlier disease history partly explains observed patters and (2) that adaptation to local host population may occur, but that direction and strength varies between populations.

21.22P

THE EVOLUTION OF MALE DIMORPHISMS IN ISLAND POPULATIONS

Joseph L. Tomkins

Division of Environmental and Evolutionary Biology, Harold Mitchell Building, The University of St Andrews, St Andrews, Fife, KY16 9TH

Male dimorphisms are likely to reflect the existence of alternative reproductive tactics. Geographic variation in selection on alternative tactics may lead to divergence in the ratio of male morphs across populations. This variation provides the ideal opportunity to examine the selection pressures that generate male dimorphisms. UK island populations of the earwig *Forficula auricularia* have a male dimorphism in forceps length that is absent from mainland populations only a few kilometres away. Furthermore, islands separated by less than 100 metres also exhibit significant divergence in male morph ratio. To test the hypothesis that demographic conditions peculiar to islands, promote the evolution of male dimorphism in this species, I quantified earwig population densities for island populations in the Northeast of Britain. These data show that increases in population density of earwigs are associated with an increase in frequency of the large male morph. To further understand the inter-population variation in sexual selection that has resulted in morph ratio divergence, I quantified the sexual selection operating on males in a number of island populations. The selection data illustrate the divergent selection in operation on the alternative male tactics on a small spatial scale in the Farne Islands archipelago.

21.23P

POPULATION GENETICS OF SPECIATION IN THE HAWAIIAN ENDEMIC PLANT GENUS *SCHIEDEA*.

Mohsen Vaez, Dmitry A. Filatov

University of Birmingham, School of Biosciences, Edgbaston, Birmingham B15 2TT, United Kingdom

The genus *Schiedea* (Caryophyllaceae) includes over thirty species endemic to Hawaii, and represents striking diversity in morphology, breeding system and habitat. This genus is a convenient model to study speciation process, since it represents one of the largest recent adaptive radiations with relatively well characterised biogeography. Here we report the level and the patterns of nuclear DNA diversity and divergence in the populations of *S. globosa* from Oahu and Maui islands. Unlike most other *Schiedea* species, *S. globosa* inhabits several islands in the Hawaiian archipelago. Phenotypic differences between the *S. globosa* plants from different islands suggest that populations of this species represent a case of on-going speciation due to colonization of several islands in the Hawaiian archipelago. Overall, the species-wide average heterozygosity per silent site (pi) is 0.3%. The silent DNA diversity on the older island of Oahu (pi = 0.24%) is almost twice higher than on the younger Maui (pi = 0.14%). Consistent with this, the haplotype phylogeny suggests a more recent origin of the Maui populations. Our data suggest that Oahu and Maui populations of this species are fairly isolated from each other ($F_{st} = 0.57$, $P<0.0001$) and that the populations are sufficiently old to recover after the founder effect, which may have followed the colonization of the islands, and to accumulate phenotypic differences in isolation, supporting Mayr's model of allopatric speciation rather than founder effect speciation models.

21.24P

LOCAL ADAPTATION AND PLANT-HERBIVORE COEVOLUTION: INTERACTIONS BETWEEN A MARINE ISOPOD AND A BROWN ALGA

Outi Vesakoski, Veijo Jormalainen, Tuija Honkanen

University of Turku, Section of Ecology, FIN-20014 Turku, Finland

The geographic mosaic theory of coevolution predicts that herbivore subpopulations are locally adapted to the variation in quality of the major host. The degree of such adaptation may vary among populations. Plants' chemical defences are assumed to play a central role in plant-herbivore coevolution. Here we studied herbivore feeding adaptations in a fragmented marine environment. We collected the herbivore *Idotea baltica* from three distinct populations of the bladder wrack (*Fucus vesiculosus*). We reared each population of *I. baltica* on alga originating from each population, and measured their performance in terms of growth and egg production. Because nutrient availability is known to affect the quality of alga for the isopods, we further manipulated the nutrient environment of the bladder wrack. The isopod populations differed in performance. Interestingly, the degree of local adaptation varied among the isopod populations. One population performed best when fed on bladder wrack originating from their home area. Another population, originating from algal belt with high level of phlorotannins, performed equally well with all origins, thus, showing capacity to tolerate defended food. On the other hand, despite of high level of phlorotannins at home area, the third population had best success with the alga having less phlorotannins. Furthermore, the isopods took advantage of nutrient manipulated alga, but again, that ability varied among the isopod origins. These results support the hypothesis, that differences in host quality may create a selective mosaic, in which also the degree of specialisation is locally variable. Thus, our results show that the geographic scale is important in the evolution of plant-herbivore interactions.

21.25P

DARK ISLANDS: SPECIATION DYNAMICS IN A HAWAI'IAN CAVE PLANTHOPPER

Andreas Wessel, Hannelore Hoch

Humboldt-Universitaet zu Berlin, Museum fuer Naturkunde, Invalidenstrasse 43, D-10115 Berlin, Germany

The cave ecosystems of Hawai'i Island provides a long sought-after model system for speciation dynamics. Spatially structured populations with different degrees of separation and isolation allow us to incorporate population structure and migration into models of speciation. Ongoing studies of the obligate cave-dwelling and highly troglomorphic planthopper *Oliarus polyphemus* revealed a young species-subspecies complex in a dynamic stage of divergence. Migration dynamics driven by succession of caves and formation of new habitats by active volcanism up to the present led to a sequence of founder events. The serial colonization of new lava flows results in the development of naturally occurring

Symposium 22

The evolutionary significance of variation in reproductive investment

Organisers: B. J. Zwaan & K. Fischer

Conference Auditorium 2

14.00 – 14.30	**Boggs, C. L.** Reproductive investment as a life history adaptation
14.30 – 15.00	**Fox, C.** The evolution of egg size and number in a variable environment: Lessons from a seed beetle.
15.00 – 15.20	**Chapman, T.** Variation in reproductive success arising from sexual conflict
15.20 – 16.00	**Tea**
16.00 – 16.20	**Kruuk, L. E. B.** Maintaining variation: the evolutionary genetics of maternal effects in a long-lived mammal
16.20 – 16.40	**Gibbs, M.** Where do good parents come from and does it matter?
16.40 – 17.00	**Candolin, U.** Condition-dependent variation in reproductive investment of male three-spined sticklebacks
17.00 – 17.20	**Fischer, K.** Artificial selection on butterfly egg size: Responses, correlated responses and fitness consequences

Invited talks

22.1

REPRODUCTIVE INVESTMENT AS A LIFE HISTORY ADAPTATION

Carol L. Boggs

Stanford University, Dept. of Biological Sciences, Stanford, CA, USA

Nutrients used in reproduction may come from larval or adult foraging, and the pattern of their allocation provides the mechanistic underpinning for life history strategies. I explore the implications of variation among species in diet and foraging habits for reproductive investment patterns, thence life history traits.

22.2

THE EVOLUTION OF EGG SIZE AND NUMBER IN A VARIABLE ENVIRONMENT: LESSONS FROM A SEED BEETLE

Charles Fox

Department of Entomology, S-225 Ag Science Center North, University of Kentucky, Lexington, KY 40546-0091

When initiating reproduction, organisms must decide both how much of their resource pool to allocate to reproduction (reproductive effort) and then how to divide these resources among offspring (offspring size versus number). Substantial theoretical attention has been paid to both of the decisions but there is little empirical data on the effect on the correlated evolution of reproductive effort and offspring size and number. Using a desert seed beetle, *Stator limbatus*, as a model system, I will illustrate how simple conceptual models of the evolution of offspring size and number, such as the Smith-Fretwell model, can adequately explain within population phenotypic plasticity in offspring size exhibited in response to variable host plant resistance. However, these conceptual models fail to explain the complex evolutionary responses to selection observed when imposing artificial selection on offspring size.

Contributed talks

22.3

VARIATION IN REPRODUCTIVE SUCCESS ARISING FROM SEXUAL CONFLICT

Tracey Chapman, Stuart Wigby

Department of Biology, University College London

In many insect species, females simultaneously store the sperm of more than one male. There is strong selection pressure therefore on males to ensure the efficient transfer, storage and use of their sperm, before it is usurped by the sperm of subsequent mates. Males should therefore be under pressure try to increase the amount of investment females put into the current mating, even if this results in a decline in the female's future reproductive investment.

Males have developed a number of ways to boost the 'per mating' reproductive investment of females. These include the transfer of seminal fluid substances that stimulate the production of eggs and produce a temporary loss of female receptivity. These substances therefore act to maximise the number of offspring fathered by the current mating male.

In the fruitfly *Drosophila melanogaster*, the use of males that lack, or have reduced levels of, specific seminal fluid (SF) substances has elucidated the role of SF in post-mating changes in female egg production and receptivity. However little is known about standing genetic variation in a male's ability to induce these responses. We are addressing this problem by employing experimental evolution in which, in replicated populations, males evolve either in competitive or non-competitive environments. We test whether seminal fluid-mediated responses differ between females mated to the resulting males.

22.4

MAINTAINING VARIATION: THE EVOLUTIONARY GENETICS OF MATERNAL EFFECTS IN A LONG-LIVED MAMMAL

[1]**Loeske E. B. Kruuk**, [1]Josephine M. Pemberton, [2]Tim H. Clutton-Brock

[1]*University of Edinburgh, ICAPB, Edinburgh EH9 3JT, UK*

[2]*University of Cambridge, Dept Zoology, Cambridge CB2 3EJ, UK*

Why is there variation in reproductive investment? Natural selection should, theoretically, result in the predominance of an optimum genotype (or genotypes) in a population, a single super-genotype producing the maximum number of highest quality offspring. However trade-offs between different components of fitness will generate variation for example, if a particular genotype can only produce many offspring of low quality or few of high quality. Such evolutionary trade-offs take the form of negative genetic correlations between two different components of reproductive investment. Despite their intuitive appeal in explaining the maintenance of genetic variation, there is surprisingly little evidence to date of negative genetic correlations between important traits, especially in natural populations. We investigated the potential for evolutionary trade-offs through an analysis of the quantitative genetics of maternal effects in a wild population of red deer (*Cervus elaphus*) on the Isle of Rum, Scotland. We focused on two phenotypic traits: offspring size (birth weight) and female fecundity. Both traits have a substantial component of additive genetic variation, as well as further variation due to maternal effects. Maternal effects on birth weight and fecundity were positively correlated, such that a mother producing large offspring will also produce relatively fecund offspring. However for birth weight there was a negative correlation between direct genetic and maternal genetic effects: genes with a direct effect of causing large birth weight in an individual also, on average, cause relatively poor maternal performance, in terms of in utero investment and hence in birth weight of that individual s offspring, and vice versa. This negative genetic correlation constitutes an evolutionary trade-off typical of the form required to maintain genetic variation in reproductive investment, and hence to maintain genetic variation in a population despite the pressures of natural selection.

22.5

WHERE DO GOOD PARENTS COME FROM AND DOES IT MATTER?

Melanie Gibbs, Allen Moore

University of Manchester, School of Biological Sciences, 3.614 Stopford Building, Oxford road, Manchester, M13 9PT, UK

Parents provide two things to their offspring genes and an environment. In some species parents provide extensive environmental effects in the form of parental care. Yet in all species with parental care there is a large amount of inter-individual variation in the quantity and quality of care provided. If providing care to offspring is beneficial, why don t all individuals increase their investment and all provide a large quantity of high quality care? By measuring both the environmental and genetic contributions of parents we aim to answer the question. Where do good parents come from and does it matter? In this study, we examine the environmental effects of parenting on life history, behaviour and morphology in the burying beetle *Nicrophorus vespilloides*. We also examine how genetics might influence variation in parental care. Male and female *N. vespilloides* parents regurgitate pre-digested food to the larvae. This parental care has important effects on offspring size and development. Variation in parental care reflects genetic and environmental influences as well. In *N. vespilloides*, indirect as well as direct genetic effects therefore influence life-history evolution. Thus indirect genetic effects may help explain why parental care is variable even when valuable.

22.6

CONDITION-DEPENDENT VARIATION IN REPRODUCTIVE INVESTMENT OF MALE THREE-SPINED STICKLEBACKS

Ulrika Candolin

Dept of Ecology & Systematics, University of Helsinki, PO Box 65, 00014 Helsinki, Finland

Male three-spined sticklebacks, *Gasterosteus aculeatus*, invest in reproduction through the establishment and maintenance of a territory, the building of a nest, the development of nuptial coloration, and the performance of courtship behaviour. Males can complete several breeding cycles and the number of cycles depends on the condition of the male at the start of the breeding season. Here I show that the investment into each breeding cycle, and the number of breeding cycles that a male completes depend on his condition at the start of the season. Males manipulated to be in poor condition invested relatively more in the first breeding cycles than males in good condition, but then died off. In contrast, males manipulated to be in good condition distributed their reproductive effort over the whole breeding season and thus completed more breeding cycles and had a larger total reproductive success. However, the large investment of poor-condition males in a few breeding cycles increased their probability of reproduction under competition with good-condition males. This demonstrates adaptive condition-dependent investment into current and future reproduction.

22.7

ARTIFICIAL SELECTION ON BUTTERFLY EGG SIZE: RESPONSES, CORRELATED RESPONSES AND FITNESS CONSEQUENCES

Klaus Fischer, Adriane N. M. Bot, Paul M. Brakefield, Bas J. Zwaan

Leiden University, P.O. Box 9516, NL-2300 RA Leiden

Egg size is a particularly interesting trait in life-history evolution because it is simultaneously a maternal and progeny character. Mothers determine egg size, which in turn can considerably affect the fitness of the progeny resulting from these eggs. To gain a more complete and integrated understanding of the evolution of this key life-history trait, we applied artificial selection using the tropical butterfly *Bicyclus anynana* as a model organism. After 11 generations of selection, lines selected for small and large eggs, respectively, differed by about 50% in egg volume with realised heritabilities (h^2) of about 0.2. Contrary to expectations, we found no correlated response in body size, development time or adult lifespan, and changes in fecundity were marginal. Reproductive investment (measured as total egg mass) increased substantially in the large egg size lines. At least under stress conditions (such as low relative humidity), larger eggs yielded a higher hatching success. Likewise, starvation resistance was higher in hatchlings originating from larger eggs. Despite of these fitness advantages of larger eggs, we did not find a clear trade-off with any other trait we investigated thus far. This leaves us with the question why there is no selection for larger eggs in the field.

Posters

22.8P

CONTEXT-DEPENDENT HONESTY: DEVELOPMENTAL PLASTICITY OF SEXUAL ADVERTISEMENT IN A PASSERINE BIRD

[1]A. V. Badyaev, [2]R. A. Duckworth

[1]*University of Arizona, 1041 E. Lowell, Tucson, AZ, 85721-0088, USA*

[2]*Duke University, Box 90338, Durham, NC, 27708, USA*

Selection for state- and context-specific investment in sexual ornamentation should favor the evolution of developmental pathways that enable the flexible allocation of resources into sexual ornamentation. We studied lifelong variation in the condition-dependence of development of a sexual ornament in relation to age and the context of breeding in male house finches *Carpodacus mexicanus* - a species that acquires a new sexual ornament once a year. The allocation of resources to the development of sexual ornamentation during molt strongly depended on pairing status in the preceding breeding season. Moreover, condition-dependence of ornamentation sharply decreased throughout a male's lifetime and in older males the development of ornamentation was largely independent of condition during molt. Our results reveal a considerable flexibility in the development of sexual ornamentation across a male's life. These findings emphasize that selection for greater elaboration of sexual displays acts on the developmental pathways that link the expression of the display with resources of the organism.

22.9P

COLONY-LEVEL LIFE HISTORY TRADE-OFFS IN THE ANT *FORMICA FUSCA*

K. Bargum, L. Sundström

University of Helsinki, P.O. Box 65, 00014 University of Helsinki, Finland

The allocation of resources into offspring is one of the key questions in life history theory. Since resources are limited, individuals face possible trade-offs between offspring size and number. Among the social insects, such trade-offs take place at the colony level, as all offspring are raised collectively by the workers, and resources can be allocated to these in different ways. Hence, under resource limitation colonies can be predicted to produce either a few large offspring, or many small offspring. We have investigated resource allocation in colonies of the black ant, *Formica fusca*. We created two different levels of resources by manipulating worker number in two-queen experimental colonies. We studied the number and size of worker offspring produced throughout the season. The results show that both offspring number and size changed with resource levels. The number of offspring was lower, and the individuals were both smaller and had a lower weight-length ratio in low-resource colonies. There was also a trade-off between offspring size and number, so that offspring size decreased linearly with increasing number of offspring. This trade-off was evident in both high-resource and low-resource colonies. The results show that worker size can be highly flexible in ants, enabling colonies to adjust the number and size of workers raised according to resource levels. Size differences between the offspring of the two nestmate queens will be investigated to reveal possible genetic or maternal factors underlying worker size variation.

22.10P

INFECTION AS A SIGNAL FOR TERMINAL INVESTMENT

[1]Camille Bonneaud, [1]Jeremy Mazuc, [2]Olivier Chastel, [1]Gabriele Sorci

[1]Laboratoire de Parasitologie Evolutive CNRS UMR 7103, Université Pierre et Marie Curie Paris 6, 7 quai St Bernard, bat A 7e etage, case 237, Paris F-75252 cedex 05, France.

[2]Céntre d'Etude Biologique de Chizé, CNRS UPR 1934 - BP14, 79360 Villiers en Bois, France.

The terminal investment theory predicts that individuals will invest more in their present reproduction if they are less likely to survive to future reproductive events. Infections, which reduce viability, may be used by individuals as an indication of a diminishing potential life span and could therefore theoretically trigger an intensification of breeding effort. However, most studies have up to now shown that immune challenges decrease feeding rates, usually resulting in a lowered reproductive output. In order to test whether diseases initiate terminal investment behaviors, we manipulated the immune system of breeding female house sparrows in a natural population by injecting them with the Newcastle Disease Virus vaccine, which elicits an antibody response. Females were captured and treated immediately after completion of their first clutch and all the eggs were removed in order to stimulate relaying. We found that challenged individuals paid a proximal cost due to immune reaction (lower yolk mass of first replacement egg, longer relaying time interval between replacement and third clutch), although this was visible only for lower quality individuals (i.e.: individuals with small brood sizes). Nevertheless, vaccinated females were more likely to lay a replacement and a third clutch and overall produced more offspring than control females. Hence, a simulated infection does appear to induce a costly terminal investment behavior. Yet intensified reproductive efforts may be delayed in the course of a breeding season as the cost of immune response may prevent individuals from immediately reacting to a decreasing life-span signal.

22.11P

DEVELOPMENTAL SENSITIVITY OF EGG PRODUCTION TO TEMPERATURE CHANGES

A. N. M. Bot, P. M. Brakefield, B. J. Zwaan

Institute of Biology, Leiden University, P.O. Box 9516, 2300 RA Leiden, the Netherlands

Females of the butterfly *Bicyclus anynana* adjust the size of the eggs they lay to the climatic circumstances they encounter. In nature they encounter a cool dry season and a warm wet season. In the laboratory there is a clear response of egg size to the temperature that the females are kept at, with larger eggs being laid at lower temperatures. Large eggs generally have a higher fitness, but females cannot produce as many large eggs as small eggs. Females are therefore trying to optimize the number of viable offspring they produce. We are interested in the genetic background of egg size and we would therefore like to know what the hormonal pathways are which regulate this trait. In order to unravel these it is necessary to know which stages of egg development are sensitive to changes in temperature. An experiment is conducted where all the eggs are counted and measured from the time on which the temperature is changed. The number of eggs produced from the temperature change up to the change in egg size can be compared with the number and stages of eggs present in the ovarioles of females that have been dissected at various intervals during the experiment. In this way the approximate stage of egg development at the temperature switch can be determined as well as changes in the ovaries that occur later on.

22.12P

VARIABLE REPRODUCTIVE INVESTMENT ALONG AN ELEVATIONAL GRADIENT IN TWO PASSERINE SPECIES

Renee A. Duckworth

Duke University, Biology Dept., Box 90338, Durham, NC 27708 USA

Altitudinal variation is a well-studied example of an environmental gradient which predictably affects the trade-off between survival and reproduction and leads to pronounced variation in life history traits and reproductive behaviors. Mountain and western bluebirds (*Sialia currucoides* and *Sialia mexicana*), are two sister species that partially co-occur along an elevational gradient. In both of these cavity-nesting species, defense of the cavity against competitors is an important determinant of fitness. However, the expression of this behavior decreases with breeding elevation in both species despite consistent pressure from competitors. In both species, social and ecological factors play an important role in modulating the expression of this behavior, however, the relative importance of specific ecological factors differs between species. I compare the expression of this behavior across elevation in areas where mountain and western bluebirds overlap to determine whether the behavioral differences between species are purely environmental or instead are due to evolution of the norms of reaction for this behavior.

22.13P

ASSOCIATION BETWEEN HOST SPECIALIZATION AND REPRODUCTIVE MODE ACROSS POPULATIONS OF THE PEA APHID, *ACYRTHOSIPHON PISUM*

A. Frantz, M. Plantegenest, N. Prunier-Leterme, J. Bonhomme, M. T. Querrien, J. C. Simon

UMR BiO3P INRA/ENSAR Domaine de la Motte 35653 Le Rheu cedex

The pea aphid, *Acyrthosiphon pisum* encompasses ecologically and genetically distinct host races specialized on various Fabaceae species. In addition *A. pisum* shows a large intraspecific diversity in reproductive modes that differ in their level of investment in the sexual phase of the annual life-cycle. Cyclical parthenogenetic (sexual) lineages alternate parthenogenetic reproduction with a sexual phase in autumn in response to decreasing photoperiod and temperature. Obligate parthenogenetic lineages (asexual) reproduce asexually all year long. In between, intermediate lineages produce both sexual and parthenogenetic forms. In aphids, sexual reproduction is often associated with plant alternation, which favours genetic admixture on one hand and could prevent host specialization on the other hand. We tested here the hypothesis that populations of pea aphids on perennial plants show a higher degree of specialization along with a smaller investment in the sexual phase than populations utilising annual plants. For that, we collected individuals in local fields of four different crops, two annual (i.e. pea and faba bean) and two perennial (i.e. alfalfa and clover). They were used to establish lineages in the laboratory whose genotypes were characterised at eight microsatellites. After removing clonal copies, we assessed the reproductive mode (i.e. sexual, asexual or intermediate) of 80 genotypes by analysing their response when placed in conditions inducing sexual reproduction. Results first showed a strong genetic differentiation between three groups of *A. pisum* : 1) from pea and faba bean, 2) from clover, and 3) from alfalfa. Second, we showed that the reproductive modes of *A. pisum* genotypes differ drastically whether they originate from perennial or annual plants. While more than 50% of genotypes on pea and faba bean belonged to sexual lineages, this type of reproductive mode represented only 10% among alfalfa and clover genotypes. The ecological and evolutionary significance of this association between host plant specialisation and reproductive mode in *A. pisum* is discussed.

22.14P

IMPORTANCE OF THE SEXUAL PHASE FOR THE MAINTENANCE OF LIFE CYCLE VARIATION IN APHIDS

F. Halkett, J. B. Bonhomme, L. Mieuzet, M. Plantegenest, J. C. Simon

UMR INRA-ENSAR BiO3P, BP 35 327, 35653 Le Rheu cedex, France

Aphids show an extremely high variability in their life cycles. This is, in particular, the case for the studied species, *Rhopalosiphum padi* in Western France where three types of reproductive modes coexist. First, cyclically parthenogenetic lineages alternate parthenogenesis (from spring to late summer) and sexual reproduction (in autumn) and have a full commitment in the production of sexual forms (males and sexual females). Because sexual females lay cold resistant eggs, such lineages do resist harsh winters. At the opposite, obligate parthenogenetic lineages sustain parthenogenetic reproduction during autumn and winter, but also produce some males occasionally. These second lineages are favoured during mild winter but are eliminated by temperature below 10°C. In between, intermediate lineages invest both in sexual and parthenogenetic reproduction during autumn (Simon et al. 2002). All those lineages thus invest in sexual reproduction but to varying degrees. The purpose of this study was to assess the ecological and evolutionary significance of the investment in sexual reproduction by each type of lineages in the field. First, we demonstrated, using molecular markers linked to the reproductive modes, that the three types of lineages may actually participate to the sexual reproduction, during autumn. Second, we showed, using biological experiments, that sexually-produced lineages that locally hatch in spring exhibit the whole spectrum of life cycle variation present in *R. padi*. Results are further discussed according to the evolutionary maintenance of the cyclical parthenogenesis in aphids.

22.15P

EGG SIZE AND YOLK CAROTENOID CONCENTRATION IN THE COLLARED FLYCATCHER (*FICEDULA ALBICOLLIS*)

[1]Rita Hargitai, [1]János Török, [1]Gábor Michl, [2]Zoltán Matus, Gyula Tóth, Gergely Hegyi, Balázs Rosivall, Beáta Szigeti

[1]*Behav. Ecol. Group, Dept. Syst. Zool. and Ecol., Eötvös Loránd University, Pázmány P. sétány 1/C., H-1117, Budapest, Hungary*

[2]*Dept. of Medical Chemistry, Medical School, University of Pécs, Szigeti u.12., H-7624, Pécs, Hungary*

The nutrients and bioactive molecules of avian egg have significant impact on the phenotype and fitness of the offspring. Egg hatchability, chick mass and viability are related to these resources provided by the mother during yolk formation. However, the deposition of these important components is costly for the mother, and may be influenced by several factors. In this study we examined the size and carotenoid concentration of collared flycatcher (*Ficedula albicollis*) eggs in relation to female age and condition, environmental factors (food supply, breeding density) and laying order. Egg volume increased with female age from young (1-, 2-year-old) to middle-aged (3-year-old), and decreased slightly thereafter. Furthermore, our results indicate that food supply influenced egg size, while the yolk carotenoid concentration was affected by the timing of egg laying. Within clutches, late-laid eggs were significantly bigger and had higher beta-carotene concentration than early-laid eggs. Carotenoids have important physiological functions in immunity and protection from oxidative damage. However, they are thought to be available in limiting amounts in nature. We suggest that the seasonal change in yolk carotenoid concentration may be the result of varying food availability. The intraclutch variation in egg size and beta-carotene concentration suggest that females invest more into the late-hatching nestlings to improve their viability and competitive abilities. Development of foraging skills as a result of experience may explain the observed increase in egg size with female age. Whereas, at older ages, the decrease in reproductive investment is probably caused by some innate deterioration of the individual.

22.16P

SELECTION FOR INCREASED BROOD SIZE IN PRE-MODERN HUMAN POPULATIONS

[1]Samuli Helle, [2]Virpi Lummaa, [3]Jukka Jokela

[1]*University of Turku, FIN-20014 Turku, Finland*

[2]*University of Cambridge, Downing Street, Cambridge CB2 3EJ, United Kingdom*

[3]*University of Oulu, FIN-90014 Oulu, Finland*

Variation in human twinning rates among populations is considered to either reflect the direct fitness effects of twinning in variable environments, or to be a maladaptive by-product of variation in other maternal reproductive traits (e.g., polyovulation). We used historical (1710-1890) data of three ecologically different Sami populations of Northern Scandinavia to contrast these alternative hypotheses. We found that women who produced twins started their reproduction younger, reproduced longer, ceased their reproduction older, and had higher total lifetime fecundity, more adult offspring, and higher fitness (individual ë) than mothers of singletons in all studied populations. This fitness advantage of twin mothers persisted even if the fitness contribution of their twin deliveries was replaced with the expected contribution of a singleton. This indicates that individual quality and propensity for twinning were coupled in these populations. In addition, an average of 1.2 offspring survived to adulthood from a twin delivery, whereas only 0.8 offspring survived from a singleton delivery. This productivity advantage of twin deliveries was independent of the sex of twins. Thus, twin deliveries were not maladaptive. Our results demonstrate the first example where twinning, irrespectively of their gender, is shown to be directly favored by natural selection in pre-modern humans.

22.17P

THE COST OF THE MALE FUNCTION IN A HERMAPHRODITIC LAND SLUG ANALYZED THROUGH LIFE-HISTORY TRAITS AND SEX ALLOCATION.

K. Jordaens, K. Temmerman, T. Backeljau

University of Antwerp, Groenenborgerlaan 171, 2020 Antwerp, Belgium

Royal Belgian Institute of Natural Sciences, Vautierstraat 10, 1000 Brussels, Belgium

The theory of resource allocation assumes that a resource not allocated to one function may be reallocated to another. In hermaphroditic organisms, an individual that suppresses the use of one sex function may automatically free resources for the other sex function. Such a reallocation of resources may occur among the different parts of the reproductive tract or among different life-history traits. Many pulmonate land gastropods and freshwater snails of the genus *Bulinus* show a genital polymorphism, i.e. phally polymorphism in which several sexual morphs co-occur: euphallics with fully developed male copulatory organs, hemiphallics in which the male copulatory organs are only partly developed and aphallics that lack male copulatory organs. We investigated if there is a reallocation from the lost male function towards the female function in the land slug *Deroceras laeve* when raised under optimal conditions. We neither observed a reallocation towards the female function in aphallic slugs, nor differences in life-history traits between eu- and aphallic individuals. This suggests a low cost for the male function under optimal conditions in this species.

22.18P

ADAPTIVE USE OF ADULT BODY RESOURCES FOR REPRODUCTION IN BUTTERFLIES

Bengt Karlsson, Fredrik Stjernholm

University of Stockholm, Dept. of Zoology, Svante Arrhenius v 14, 106 91 Stockholm, Sweden

Reproductive patterns in butterflies as well as in other organisms are often constrained by nutritional reserves, necessitating trade-offs between reproduction and other non-reproductive needs. In most adult butterflies the diet consists mainly of carbohydrates and water, while reproductive products contain a high proportion of nitrogenous products. Thus, butterflies, especially females but sometimes also males, are limited by stored larval derived body reserves of nitrogen for their reproduction. Most of these reserves are stored in the abdomen and is thus the major source for reproductive products (eggs and spermatophores). However, recent observations showing that thorax resources in butterflies decrease as they age might be an indication of that butterfly females also use flight muscles as an indirect resource in egg production. For some species with a nuptial gift giving system this might also be possible for males in the production of spermatophores. In support for this idea, we have observed that thorax nitrogen content decline with age in natural populations, and budget calculations support that a substantial part of a female s reproductive nutrient pool comes from the thorax. Since thorax consists mainly of flight muscles, flight performance (e.g. manoeuvrability) might be affected. These possibilities are discussed and result from recent studies presented.

22.19P

GRANDMOTHERING: BENEFICIAL REPRODUCTIVE INVESTMENT TACTIC IN PRE-INDUSTRIAL HUMANS

[2]Mirkka Lahdenperä, [1]Virpi Lummaa, [2]Samuli Helle, [2]Jenni Pettay

[1]*Department of Zoology, University of Cambridge, Downing Street, Cambridge, United Kingdom*

[2]*Section of Ecology, Department of Biology, University of Turku, Finland*

In a few species, including humans, females become reproductively sterile (menopause), and yet live for several years after this point. The Grandmother Hypothesis predicts that menopause is an adaptive reproductive tactic, in which females with low probability of further success cease reproducing in order to concentrate on increasing the reproductive potential of daughters and survival of grand-offspring. Here we used individual-based demographic records of 18th-19th century Finnish people to investigate the fitness benefits of grandmothering. We studied the importance of grandmothering by examining the impact of grandmothers on: (1) key life-history traits and fitness (fecundity, lifetime reproductive success and individual lambda) of their reproductive sons and daughters; (2) the survival of their grandchildren; and (3) the relationship between post-reproductive longevity and total number of grandchildren produced. Our results show that the presence of a grandmother had a positive effect on both the fitness of her reproducing offspring (increased fecundity, LRS and lambda) and the survival of her grandchildren early in life. Although a living grandmother improved the survival of her grandchildren, grandmothers increased their own fitness primarily through reducing the age at which their offspring first started reproducing and the subsequent rate at which they produced children throughout their reproductive lifespan. Finally, the longer the grandmother lived after she last gave birth herself, the more grandchildren she had. These results show that grandmothers had an essential role in assisting their offspring to reproduce successfully, and prolonged post-reproductive lifespan improved female fitness by increasing the number of grandchildren born to her.

22.20P

PARENTAL CARE, MATERNAL EFFECTS AND LIFETIME REPRODUCTIVE SUCCESS IN A COOPERATIVE BREEDER.

Andrew MacColl

University of Sheffield, Animal and Plant Sciences S10 2 TN, Sheffield, UK

Substantial recent attention has focussed on the importance of maternal effects in evolution. Parental care, an important source of maternal effects, has traditionally been considered to form part of the environmental effects on the phenotypes of offspring in the quantitative genetic analysis of trait evolution. However where these 'environmental effects' are under partial genetic control they may themselves evolve. In species with complex social systems, such as cooperative breeders, where the quality of the offspring environment may depend largely on the care of related individuals, maternal effects may be of special importance. Here we show that a heritable measure of parental care increases lifetime reproductive success of offspring in a cooperatively breeding bird, the long-tailed tit. We examine the potential significance of our measure of care for morphological evolution.

22.21P

MATERNAL EFFECTS AND THE RESPONSE TO SELECTION IN RED SQUIRRELS

[1,2]Andrew G. McAdam, [1]Stan Boutin

[1]*Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada. T6G 2E9*

[2]*Department of Ecology and Evolutionary Biology, Earth and Marine Sciences Building, University of California, Santa Cruz, CA 95064, USA*

Models of maternal effect evolution predict that the response to selection in the current generation can be accelerated or dampened by genetically based maternal effects and can be influenced by selection in previous generations. We have previously quantified direct and maternal genetic effects on juvenile growth rates in a natural population of red squirrels (*Tamiasciurus hudsonicus*) using cross-fostering experiments. In addition, we have estimated viability selection on 13 cohorts of juveniles since 1989. Changes in growth rates of squirrels across one generation of selection (Rt) were significantly correlated with the strength of selection in the current generation (St) and revealed a realised heritability that was much greater than the previous estimate based on direct genetic effects alone, but was similar to the total heritability estimate that included the contribution of maternal effects. Furthermore, the response of juvenile growth rates in the current generation (Rt) was not independent of selection in the previous generation (St-1). These results are consistent with a significant contribution of maternal effects to the evolutionary dynamics of growth rates in juvenile red squirrels.

22.22P

REPRODUCTIVE SKEW AND CRYPTIC SPECIES IN FIG WASPS: IMPLICATIONS FOR SEX RATIO ADAPTATION.

[1,2]Drude Molbo, [2]Laurent Keller, [3]Edward Allen Herre

[1]*Smithsonian Tropical Research Institute, Unit 0948, APO AA34002, USA*

[2]*Edinburgh University, ICAPB, Kings buildings, West Mains Road, Edinburgh EH93JT, Scotland UK*

[3]*University of Lausanne, IE-ZEA, BB, 1015 Lausanne, Switzerland*

[4]*Smithsonian Tropical Research Institute, Unit 0948, APO AA34002, USA*

The sex ratios of fig wasps have often been used to test sex ratio theory such as local mate competition theory (LMC). These tests were based on a few simple assumptions. We have recently discovered that these assumptions often were wrong, including the assumption of one-to-one species specificity between wasps and figs (Molbo et al 2002, in press). In fact, several fig species hosted sympatric pollinator species and these species were laying eggs in the same individual fruits. Under LMC, the optimal sex ratio a foundress wasp should produce depends not only on her own brood size but on her relative contribution to the future local mating group. We present sex ratios produced by individual fig wasp foundresses in nature. Offspring wasps reared out of fruits were separated into sibhoods using microsatellite genetic markers. Sex ratios of individual foundresses sharing fruits with non-reproducing or reproducing, conspecific or allospecific co-foundresses were related to several aspects of precision of adaptation: First, the selective pressure for an optimal behaviour should vary with how frequently that behaviour is needed in nature. Second, selective pressure should increase with the relative fitness gained from the optimal behaviour relative to any less optimal behaviour or the cost of making errors. Third, the information available to a foundress and her ability to respond accurately impose limits on the adaptive precision. The different relative frequencies of pollinator species and differences in foundress number distributions across species lead to different expectations of optimal behaviour for foundresses of different species and provides us with a tool to distinguish between these different effects.

22.23P

MANIPULATION OF OFFSPRING NUMBER AND SIZE: BENEFITS OF LARGE BODY SIZE AT BIRTH DEPEND UPON THE REARING ENVIRONMENT

T. A. Oksanen, I. Jokinen, E. Koskela, T. Mappes, H. Vilpas

Department of Biological and Environmental Science, P.O. Box 35 (YAC), FIN40014 University of Jyväskylä, Finland

Allocation of reproductive effort between the number and size of offspring determines the immediate rearing environment for the growing young. As the number of offspring increases, the amount of parental investment per individual offspring decreases, and the quality of the rearing environment is expected to decrease. This may result in a lower quality of offspring reared in such conditions. We studied the effects of the rearing environment on the quality of juvenile bank voles, *Clethrionomys glareolus*, with different initial body sizes at birth in a 2 x 2 factorial experiment. The rearing environment was manipulated by enlarging both the litter size by two extra pups, and mean offspring body size at birth by replacing the original litter with heavier pups from smaller litters. Offspring quality was estimated from body size measurements, parasitic infection with *Eimeria* spp. and the level of immune response to a novel antigen. The analyses revealed that large body size at birth was an advantage in normal rearing environments, but a disadvantage in poor ones. The initially normal sized offspring grown in enlarged litters had a relatively good capacity for growth and high immune function confirming that a poor rearing environment alone does not reduce their quality. Our findings that the benefits of large body size depend on the rearing environment suggest that offspring body size is adjusted in relation to litter size, and thus the evolution of these two traits is combined.

22.24P

DO HERBIVORES INCREASE REPRODUCTIVE INVESTMENT IN A PERENNIAL HERB, *SEDUM MAXIMUM*?

Pawel Olejniczak, Pawel Adamski

Institute of Nature Conservation PAS, Mickiewicza 33, 31-120 Krakow, Poland

One of the most intriguing phenomena concerning inter-specific effects on plants is a positive effect of herbivores on plant reproductive performance. The issue has been extensively discussed and often questioned: why should a plant limit its lifetime reproduction in the absence of herbivores and devote more resources into offspring in case of being grazed? This mutualistic effect of herbivory on plant reproduction (overcompensation) has been convincingly reported only few times. All the reports concern annual or biennial plants. Here I present an experiment to show whether grazing can stimulate seed production in a perennial *Sedum maximum*. More than 200 individuals of *S. maximum* were selected, marked and measured in their natural localities in The Pieniny Mountains, southern Poland. They were assigned at random to two groups. Apical buds were clipped in half of them to imitate the effect of herbivores and other half was left as a control. There were no initial differences between the groups in any of the measurement (stem diameter, length of shoot etc.). At the end of the season all shoots and inflorescence were measured, fruit were weighed and seeds were examined for germination ability. Clipped plants were found to produce more inflorescences and the total mass of fruit was significantly greater than non-clipped plans. The manipulation had no negative effects on seed size, germination rate or below-ground biomass. The results indicate that *S. maximum* can increase reproductive investment in a year of manipulation as a result of apical bud removal. This can be explained either as a real positive effect of herbivores on the plant or as a change in age-specific reproductive allocation at the expense of reproduction in following seasons. However, no effect of clipping on overwintering root biomass is in favor of the first explanation.

22.25P

GENETIC VARIATION IN THE TOLERANCE OF THE COST OF REPRODUCTION IN MALE *CALLOSOBRUCHUS MACULATUS*

Satu Paukku, Janne S. Kotiaho

Department of Biological and Environmental Science, P.O.Box 35, 40014 University of Jyväskylä, Finland

The aim of reproduction is to produce highest possible number of viable descendants. Because reproduction utilizes resources that are limited, reproduction affects negatively other life-history traits, thus reducing fitness and causing a cost of reproduction. The aim of this study was to determine, whether there is the cost of reproduction and whether there is genetic variation in the tolerance of the cost of reproduction in *Callosobruchus maculatus* males. Unmated males survived longer than four times mated males in both parent and offspring generations. This demonstrates a cost of reproduction. Significant interaction between genotype and mating treatment demonstrated that there was genetic variation in the tolerance of the cost of reproduction. Negative correlation between baseline longevity and the cost of reproduction for each family indicated that there may be a continuum of different strategies between genotypes. Our results clearly show that there is potential for evolution in trade-offs of reproduction.

22.26P

EGG QUALITY, HATCHING ORDER AND CHICK PERFORMANCE IN MAGPIES.

Marjo K. Pihlaja, Heli Siitari, Rauno V. Alatalo, Jonna Timonen

University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FIN-40014 University of Jyväskylä, Finland

We are interested in the effects of egg quality and hatching order on chick's performance in magpies (*Pica pica*). Clutch size of magpie is relatively large; 5-10 eggs (mean 7.5 eggs) and hatching is asynchronous. Only about 30% of hatchlings will fledge, and the surviving chicks are most commonly the first hatched ones. Our previous study indicates that several parameters revealing egg quality change within the laying order. In spring 2003 we are investigating experimentally the effects of hatching order on survival and growth of magpie chicks. We will have two experiment groups; one group is containing nests where first two chicks will be fostered to another nest to place last two chicks of the same age. The last two chicks of the foster nest are then moved to third nest to place its firs two chicks of the same age and so on. In the other group we will change two chicks randomly between nests without changing their original position within the clutch to control the effects of cross-fostering. In addition to laying and hatching order effects, we will follow growth, survival and several condition measures of the chicks until fledging. With this experiment we are then able to separate effectively the effects of hatching order and egg quality on chick performance.

22.27P

INVESTING IN CURRENT VS FUTURE REPRODUCTION: WHAT PRICE TO PAY?

A. Rivero, S. A. West

Institute of Cell, Animal and Population Biology, University of Edinburgh, Kings Buildings, Edinburgh EH9 3JT

One of the systems where the connection between the evolutionary and physiological aspects of reproductive investment has been most explicitly made is in parasitic wasps (parasitoids). In most species of parasitoids, the females face a puzzling reproductive conflict. Their eggs must be laid on the body of a good quality host for their offspring to develop (offspring fitness is directly correlated with host quality). However, these same hosts represent the only source of proteins available to the females to produce eggs in the first place. In order to avoid reducing the quality of the host for their developing offspring, some species have chosen to host-feed and lay eggs in different hosts. However, almost half of the known species of host feeding parasitoids use the same host for feeding and for oviposition. On encountering a host, these females are thus faced with a dilemma: how much nutrients should they extract from the host in order to boost their future reproductive opportunities and minimise the costs to their offspring? We manipulated the host feeding behaviour of the parasitoid *Nasonia vitripennis* and quantified the resulting fitness costs and benefits. Our results show that while the benefits of host feeding are straightforward (egg production increases) the costs of host feeding are dependent on the clutch size and sex ratio of the brood. Because of asymmetric competition between the sexes, female offspring suffer disproportionately the costs of host feeding, particularly in more male-biased broods.

22.28P

DIETARY GLYCEROL AND ADULT ACCESS TO WATER: EFFECTS ON FECUNDITY AND LONGEVITY IN THE ALMOND MOTH

[1]C. Ryne, [1]P. A. Nilsson, [2]M. T. Siva-Jothy

[1]Lund University, Div of Ecology, Solveg. 37 SE-223 62 Lund, Sweden

[2]University of Sheffield, Animal and Plant Sciences S10 2 TN, Sheffield, UK

The quality of the food eaten by larvae sets the standard for the adult insect in terms of gamete production, fat reserves and muscle tissue. The almond moth (*Ephestia cautella*) (W.) (Lepidoptera; Pyralidae) is non-feeding as an adult, however, it does drink water. The larva is also dependent on high moisture content in the diet for survival. The adult almond moth could by drinking water, hypothetically, even out poor (dry) quality food eaten as larvae. We tested this idea by rearing larvae on two different food sources with different moisture; standard laboratory diet with glycerol (good quality) and standard diet without glycerol (poor (dry) quality). Half of the adult moths from each larval diet were then given water to drink before the first mating. All adults were allowed to mate only once. Surprisingly, results show that glycerol in the larval food significantly decreased the fecundity and increased the male and female longevity. The interaction effect of water access for adult males and females was significant, independent of the glycerol in the diet. Longevity in females not receiving water was slightly higher if mated with a male that had had access to water. For females that had received water, the trend was opposite; longevity was lower if mated with a water male. When larval diet includes glycerol, an increased number of eggs laid decreases the longevity of the female. However, when no glycerol is present in the larval diet, the number of eggs she oviposits does not affect female longevity. We discuss the possibility that this is a diet-induced opportunity for reproductive decisions in the first mating by the female that depends on the quality of the food she receives as larva. Females with high quality food may enjoy increased longevity and thereby more mating occasions and higher fitness.

22.29P

SEASONAL TRENDS OF BIRTH SEX RATIO IN ZZ/ZW AND XX/XY POPULATIONS OF JAPANESE FROG, *RANA RUGOSA*

[1]Y. Sakisaka, [2]I. Miura, [3]E. Kasuya, [3]T. Yahara

[1]*Shinsyu University, Matsumoto, Nagano, 390-8621, Japan*

[2]*Hiroshima University, Higashi-hiroshima, Hiroshima, 739-8526, Japan*

[3]*Kyushu University, Fukuoka, Fukuoka, 812-8581, Japan*

In vertebrates having sex chromosomes, it had been believed that parents cannot control offspring sex ratio. However, a few empirical studies have shown that parents of some birds and mammals do control sex ratio. Here, we report the first example of seasonal shift of primary sex ratio in amphibians. In *Rana rugosa*, there are two morphs differing in sex determination system, ZZ/ZW (female heterogamety) and XX/XY (male heterogamety). This divides the species into two geographical morphs. We studied the seasonal trends of the sex ratio at birth in two natural populations by using molecular techniques. The eggs in a ZZ/ZW population and a XX/XY population were sampled in the field from May to August in 1998, and from June to August in 1999, respectively. Each egg was then sexed by polymerase chain reaction-restriction fragment length polymorphism (PCR-RFLP) using a sex-specific DNA marker. We found that the gradual seasonal changes of sex ratio in both frog populations. Because *R. rugosa* is a species of external fertilization, sex ratio change in a ZZ/ZW population is attributed to mother's control. In addition, we suggest that fathers may control sex ratio in a XX/XY population.

22.30P

PLASTICITY IN MATERNAL INVESTMENT IN A SPIDER WITH SUICIDAL MATERNAL CARE

[1]Mor Salomon, [2]Jutta Schneider, [3]Yael Lubin

[1]*Life Sciences Department and Mitrani Department of Desert Ecology, Ben-Gurion University, Israel*

[2]*Institute of Evolutionary Biology and Ecology, University of Bonn, Germany.*

[3]*Mitrani Department of Desert Ecology, Ben-Gurion University, Israel*

Parental care is usually related to high investment per offspring. The manner in which maternal resources are partitioned to the young may influence their size at adulthood and ultimately, their fitness. Plasticity in the female s ability to provide maternal resources to the young should result in optimal fitness of the young. Parental care is relatively uncommon among invertebrates, but occurs in several spider families. Female *Stegodyphus lineatus* (Araneae, Eresidae) are semelparous, produce a single small clutch containing small eggs, and provide the young with additional energy by regurgitating digested material and by providing her body as food (matriphagy). Parent-offspring conflict may lead to plasticity in resource allocation. Each offspring is expected to maximize the amount of food it obtains from the female, however the female may prefer to conserve her resources for a replacement clutch in case of predation or to divide her resources evenly between her offspring. We asked whether females vary the allocation of resources to regurgitation and matriphagy? Fewer resources were provided during regurgitation (41% of total female mass) than during matriphagy (54%). The reason for this may be physiological constraints on the mobilization of food for regurgitation. Females with experimentally reduced brood size gave only 13% of their body mass in regurgitation, which caused matriphagy to be delayed. Females with experimentally increased brood size increased the percentage of food provided at regurgitation at the expense of resources reserved for matriphagy, however matriphagy did not occur much earlier than expected. It is not known if the amount of food provided at regurgitation is controlled by the female or by the young.

22.31P

ARRIVAL FAT PREDICTS IMMUNE COMPETENCE AND BREEDING SUCCESS OF PIED FLYCATCHERS (*FICEDULA HYPOLEUCA*)

[1]Roland Sandberg, [2]Mare Lõhmus, Thomas Andersson, Björn Holmquist

[1]*Department of Ecology, Animal Ecology, University of Lund, Ecology Building, SE-223 62 Lund, Sweden.*

[2]*Department of Zoology/Zoomorphology, Göteborg University, Box 463, SE-405 30 Göteborg, Sweden*

Long-distance passerine migrants deposit large fat stores to fuel their migratory journeys. Many of those migrants arrive at their breeding grounds with fat stores to spare. It is well established that the pre-breeding nutritional condition of parent birds affects breeding success. Such an effect is most dramatic among waterfowl that breed at high latitudes and rely almost exclusively on pre-stored fat to produce a complete clutch of eggs. The influence of arrival condition on reproductive performance in long-distance migrating passerines is virtually unknown. In this paper we show for the first time that arrival fat load acts as an important predictor of reproductive success among long-distance migrating Pied Flycatchers breeding close to the Arctic Circle, in northern Sweden. We found that arrival fat stores of female Pied Fycatchers were significantly correlated with: (a) date of first egg, (b) number of hatched eggs, (c) number of young reaching 7 days of age, and (d) the number of grams of produced young/breeding attempt (i.e. reproductive success). We also considered the possibility that female Pied Flycatchers that arrive with surplus fat stores may be of a higher phenotypical quality, by testing their T-cell response, and were able to show that fat females show a significantly higher immune response that do lean females. These data lead us to believe that arrival fat constitutes an important predictor of the overall phenotypical quality of a female and her breeding performance.

22.32P

VARIATION IN REPRODUCTIVE STRATEGIES AND THE CLIMATIC ENVIRONMENT: A COMPARATIVE ANALYSIS USING DEMOGRAPHIC TIME SERIES OF SEABIRDS

Hanno Sandvik

University of Tromsø, Dept of Biology, 9037 Tromsø, Norway

Among species of seabirds there is an amazing variation in life-history tactics: clutch sizes range for instance from one egg every second year to six eggs per year, adult annual survival rates vary between 75% and well above 95%. Those species all live in marine habitats, which are known for their high degree of environmental stochasticity. Life-history theory predicts that environmental variability favours strategies that do not jeopardise future reproduction by investing too heavily into current offspring. However, it is still poorly understood how different life-history strategies affect the species' response to long-term changes in the mean and variance of environmental variables. I conducted a comparative study of seabirds' responses to climatic variability. Published demographic data from all taxa of seabirds from all climatic regions of the globe were used to analyse patterns of response to climatic oscillations, as measured by climate indexes (such as the El Niño-Southern Oscillation index, ENSO, the North Atlantic Oscillation index, NAO, or the North Pacific index, NP). The analysis of this interspecific database yields insights into the correlated evolution of reproductive traits along different branches of the avian phylogeny. Some preliminary findings of those analyses will be presented.

22.33P

DO BLOOD PARASITES MEDIATE SURVIVAL COSTS OF REPRODUCTION IN THE BLUE TIT (*PARUS CAERULEUS*)?

Martin Stjernman, Jan-Åke Nilsson, Lars Råberg

Lund University/Dep. of Animal Ecology, Ecology building, 223 62 Lund, Sweden

It has been suggested that the trade-off between current reproductive effort and future reproductive success could be mediated by parasites. To test this hypothesis, the relation between manipulated reproductive effort and parasitism as well as the relation between parasitism and fitness has been investigated. Since many parasites (especially blood parasites) are not amenable to direct manipulation, the later studies have been correlational. There is, however, a problem of causality with such an approach. The manipulation might, through a third factor, simultaneously affect both parasite status and survival. An alternative approach is to use path analysis to investigate the relative importance of different paths (such as that through parasite status) in affecting survival. In this study such an analysis has been performed in a system with the blue tit (*Parus caeruleus*) as the host and *Haemoproteus majoris* as the parasite. The results show that although the manipulation of reproductive effort was related to survival in the predicted way there was no evidence that this effect was mediated by blood parasites. Moreover, there were differences related to age in the response to the manipulation of reproductive effort on parasites status suggesting that age classes differ in their ability to control parasites.

22.34P

YOLK COLOUR REFLECTS FATHER S PLUMAGE COLOUR IN GREAT TIT *PARUS MAJOR*

B. Szigeti, J. Török, R. Hargitai, G. Hegyi, B. Rosivall, G. Michl

Behav. Ecol. Group, Dept. of Syst. Zool. & Ecol., Eötvös Loránd University, Pázmány P. s. 1/c, 1117 Budapest, Hungary

In order to test good genes model of sexual selection, potentially confounding maternal effects on offspring viability should be controlled for. These effects can occur as early as before egg laying, yet maternal differential investment into eggs are rarely taken into account. Carotenoids, which occur both in egg yolk and feathers of great tits, are known to enhance immune defence and reduce oxidative stress, moreover, these beneficial effects are most pronounced in reddish forms. We scored yolk colour of eggs in 19 clutches of a wild great tit population, and measured some morphological and plumage variables of parent birds. Since yolk colour variation showed no within clutch tendency, we used average scores of clutches. We found that none of the female caracteristics (age, body condition, chest yellowness and breast stripe size) was related to yolk colour. Among male traits, in contrast, male chest plumage hue, controlled for male age, showed a significant positive correlation with average yolk colour score. Since chest yellowness may reflect individual quality in great tits, this result can be interpreted as a preferential female investment. However, male breast stripe size which functions as a mate choice cue, did not correlate with yolk scores. To our knowledge, this is the first study to demonstrate differential maternal carotenoid investment in eggs in relation to a carotenoid-based colour signal of the mate.

22.35P

VARIATION IN REPRODUCTIVE INVESTMENT IN THE SPRINGTAIL *FOLSOMIA CANDIDA* IN RELATION TO GENETIC AND ENVIRONMENTAL FACTORS

[1]Thomas Tully, [1]Regis Ferriere, [2]Tom Van Dooren

[1]*Laboratoire d'Ecologie - UMR7625, Ecole Normale Superieure, 46 rue d'Ulm, 75230 Paris Cedex 05, France*

[2]*Leiden University, Institute for Evolutionary and Ecological Sciences, P.O. Box 9516, 2300 RA Leiden, The Netherlands*

In order to address some of the fundamental questions raised in this session, we have studied reproductive investment in laboratory populations of the parthenogenetic springtail *Folsomia candida*. In order to disentangle the genetic and environmental factors that determine variation in reproductive investment we have used eleven genetically distinct clonal strains from Europe and North America. Variation in their reproductive investment was assessed by contrasting controlled environments with two different levels of food availability. After having controlled for maternal effects, these individuals were followed from their birth to their natural death and many aspects of their reproductive investment were recorded (age at maturity, date of clutch laying, number, size and fertility of the eggs layed, lifetime reproductive success) as well as their size, growth rate and longevity. We found that the levels, patterns and plasticity of investment in reproduction were very different between the clones and that this variation was linked to differences in other life history traits such as senescence.

22.36P

THE DYNAMICS OF MALE BROODING, MATING PATTERNS AND SEX-ROLES IN PIPEFISHES AND SEAHORSES (FAMILY SYNGNATHIDAE)

[1]Anthony B. Wilson, [2]Ingrid Ahnesjö, [3]Amanda C. J. Vincent, [4]Axel Meyer

[1]*Northwest Fisheries Science Center, 2725 Montlake Blvd, East, Seattle, Washington, 98112, USA*

[2]*Department of Animal Ecology, Evolutionary Biology Centre, Uppsala University, Noryvägen 18D, S-752 36 Uppsala, Sweden*

[3]*Project Seahorse, Fisheries Centre, The University of British Columbia, 2204 Main Mall, Vancouver, B.C. V6T 1Z4, Canada*

[4]*Department of Biology, University of Konstanz, 78457, Konstanz, Germany*

Modern theory views the relative parental investment of the sexes in their young as a key factor responsible for sexual selection. Seahorses and pipefishes (family Syngnathidae) are extraordinary amongst fishes in their remarkable adaptations for paternal care and frequent occurrences of sex-role reversals (i.e. female-female competition for mates), offering exceptional opportunities to test fundamental predictions of sexual selection theory. During mating, the female transfers eggs into or onto specialized egg-brooding structures that are located on either the male s abdomen or its tail, where they are osmoregulated, aerated and nourished during their development. All syngnathid males exhibit this form of parental care but brooding structures vary, ranging from the simple ventral gluing areas of some pipefishes to the completely enclosed pouches found in seahorses. Mapping male pouch types on a molecular phylogeny for syngnathid fishes indicates that pouch diversification has been positively correlated with a major evolutionary radiation of the group, suggesting that this extreme development and diversification of paternal care may have been an important evolutionary innovation of the Syngnathidae. Based on several recent studies that suggest that the complexity of male brooding structures reflects the degree of paternal investment, sex-role reversals were expected to be more common among species with highly developed brooding structures. In contrast to this prediction, however, parsimony- and likelihood-based reconstructions of the evolution of sex-role reversal in these fishes suggest multiple shifts in sex-roles in the group, independent of the degree of brood pouch development. At the same time, our data demonstrate that sex-role reversal is positively associated with polygamous mating patterns while most non-reversed species mate monogamously, suggesting that selection for polygamy or monogamy in pipefishes and seahorses may strongly influence sex-roles in the wild.

22.37P

GENETIC VS. FUNCTIONAL TRADEOFFS IN COST OF REPRODUCTION

Shin-ichi Yanagi, Takuro Oikawa, Takahisa Miyatake

Okayama University, Fac. Agric., Tsushima-naka 1-1-1, 700-8530 Okayama, Japan

We will briefly review the research history of the measurement of cost of reproduction, and then introduce our up-to-date results of sib-analysis on life-history parameters conducted under different degrees of cost of reproduction in the adzuki bean beetle, *Callosobruchus chinensis*. The inspection of cost of reproduction can be attained by detection of tradeoffs between reproduction and survival. There was a controversy about the methodology to detect the tradeoffs in 1980s-90s. The main point of issue was whether the response to experimental manipulation was equal to the evolutionary response to selection or not. We here employed a combo-experimental design of half-sib analysis and environmental manipulation to detect cost of reproduction using a laboratory population of *C. chinensis*. This design was set up to explore an empirical relationship between evolutionary direction and phenotypic plasticity, and then could resolve the controversy described above. We estimated genetic correlations across environments for longevity under the two environmental conditions, no-cost and cost of reproduction, in both female and male. The longevity was longer under the former than the latter condition in both sexes, indicating that the functional tradeoffs were detected. However, genetic correlations across environments were significantly different from one in female, but not in male. The phenotypic plasticity in manipulation experiment (=functional tradeoffs) had a genetic base in female but not in male. In addition, we estimated genetic correlation between fecundity and longevity in female under cost of reproduction. The genetic correlation was significantly higher than zero. Then, the phenotypic plasticity in experimental manipulation was not equal to the evolutionary response to selection: the direction of functional tradeoff in female was different from that of genetic tradeoff, after all. So, it is quite right that we need the quantitative genetic approach to predict any evolutionary response to selection.

Symposium 23

Morphological model systems in evolution and development

Organisers: Christian Klingenberg & Benedikt Hallgrímsson

Roger Stevens Lecture Theatre 20

14.00 – 14.30	**Hall, B. K.** Cell condensations as modules of morphological change in development and evolution
14.30 – 15.00	**Cheverud, J. M.** Modular structure of pleiotropic effects on morphology
15.00 – 15.20	**German, R. Z.** Variation in growth of the craniofacial skeleton
15.20 – 16.00	**Tea**
16.00 – 16.20	**Leamy, L. J.** Epistatic pleiotropy within and between early- and late-developing skull character complexes in mice
16.20 – 16.40	**Richtsmeier, J. T.** Developmental instability of the skull in aneuploidy
16.40 – 17.00	**Hallgrimsson, B.** The use of mouse mutant models for understanding canalization and developmental stability
17.00 – 17.20	**Renaud, S.** Morphological variability in mandible shape of wood mice (*Apodemus*): Latitudinal gradients as adaptive trend?

Invited talks

23.1

CELL CONDENSATIONS AS MODULES OF MORPHOLOGICAL CHANGE IN DEVELOPMENT AND EVOLUTION

Brian K Hall

Biology Department, Dalhousie University, Halifax, NS Canada B3H 4J1

The phenotype cannot be read from the genotype in any simple one-to-one relationship. Indeed, more than one phenotype can arise from a single genotype, as exemplified in phenotypic plasticity. Therefore, the processes of embryogenesis, development and life history effect the transition from genotype to phenotype. These processes, however, are often depicted as a black box between the genotype and the features (structures, functions, behaviors) of the phenotype. I will emphasize the important role of cells, especially aggregations of like cells, in translating and transforming genotype to phenotype. I do not downplay the role of genes but place genes in context. As development ensues, multicellular assemblages of like cells (modules) progressively appear — germ layers, embryonic fields and condensations — in a hierarchy of changing roles. As modules, condensations are fundamental developmental (morphogenetic) units that form the tissues and organs from which the structural elements of the phenotype are constructed in any one individuals. Condensations are also selectable units of morphology (or at the very least, units that mediate the response to selection at higher levels) that function as evolutionary developmental mechanisms to effect phenotypic changes between generations. In a hierarchy of emergent processes, gene networks and gene cascades (genetic modules) link the genotype with morphogenetic units such as condensations, while epigenetic processes such as embryonic inductions, tissue interactions and functional integration, link morphogenetic units to the phenotype. I will provide some historical background to the search for fundamental cellular units (a search which began over 150 years ago) and theories of morphological change in evolution. The concept of cells as modular morphogenetic units in development and in evolution will be illustrated with a specific example, the modules from which the vertebrate skeleton is constructed and by which it evolves. Supported by grants from NSERC (Canada), the Canada Council Killam Trust and Dalhousie University.

23.2

MODULAR STRUCTURE OF PLEIOTROPIC EFFECTS ON MORPHOLOGY

James M. Cheverud

Washington University School of Medicine, 660 S. Euclid Avenue, St. Louis, Missouri, USA

The genetic variance/covariance matrix of an evolving population mediates the coordinated evolutionary response of morphological features to natural selection and genetic drift. The level of co-inheritance of features, measured by the genetic covariance, arises, in part, from the pleiotropic patterns of gene effects. Individual gene loci may affect a variety of features. We have discovered that the pattern of pleiotropic effects is modular, with pleiotropic gene effects generally being restricted to developmental and functional morphological modules. We have only rarely discovered evidence for antagonistic pleiotropy suggesting a trade-off between modules. This modular pleiotropic pattern is illustrated in quantitative trait locus studies of body size growth, body composition, cranial morphology, and mandibular morphology. However, these pleiotropic patterns need not be static but may evolve. Evidence for genetic variation in pleiotropic relationships between total mandible length and regional mandibular morphology is presented. This genetic variation allows the evolution of pleiotropy under selection.

Contributed talks

23.3

VARIATION IN GROWTH OF THE CRANIOFACIAL SKELETON

R. Z. German

University of Cincinnati, Dept Biological Sciences, Cincinnati, OH 45221-0006 USA

Variation in the rates and timing of growth is a potent source of raw material for morphological evolution. Small changes in a growth trajectory can have a large impact on the ultimate and adult size of an animal. Yet little is known about the existing or potential variation in patterns of postnatal development. Working with inbred rats, we documented the variation in craniofacial growth generated by two different nutritional insults: diabetes and protein malnutrition. The data were longitudinal, which permitted high-resolution measurement of the patterns of growth within an individual. We found significant differences in the craniofacial skeletal growth response to diabetes between males and females relative to the same sex control. Protein malnutrition also produced tremendous variation in growth between dietary groups, as well as differences in life history and reproductive parameters. In addition to between group variation, these insults significantly increased within group variation; the controls have very limited variation in craniofacial skeletal growth parameters, but the experimentals are significantly more variable. These results suggest that even when the "normal" genetic variation appears reduced, as is true of inbred strains of laboratory animals, environmental perturbation can elicit extensive variation in craniofacial growth.

23.4

EPISTATIC PLEIOTROPY WITHIN AND BETWEEN EARLY- AND LATE-DEVELOPING SKULL CHARACTER COMPLEXES IN MICE

[1]**Larry J. Leamy**, [2]Jason B. Wolf, [3]Eric J. Routman, [4]James M.Cheverud

[1]University of North Carolina at Charlotte, Department of Biology, Charlotte, NC 28223, U.S.A.

[2]University of Tennessee, Department of Ecology and Evolutionary Biology, Knoxville, TN 37996, U.S.A.

[3]San Francisco State University, Department of Biology, San Francisco, CA 94132, U.S.A.

[4]Washington University School of Medicine, Department of Anatomy and Neurobiology, St. Louis, MO 63110, U.S.A.

Although single-locus pleiotropic effects are assumed to be the primary cause of associations of characters, especially in developmentally or functionally-integrated character complexes, two-locus epistatic effects can also generate such associations. We tested for the relative importance of this "epistatic pleiotropy" in producing correlations within and among early- and late-developing murine skull characters. QTLs affecting a set of eight skull characters that were unambiguously classified as either early- (3 characters) or late-developing (5 characters) were mapped in a population of mice derived from an original intercross of the Large and Small inbred strains. Significant epistasis was found for a number of pairwise combinations of 21 quantitative trait loci (QTLs) affecting the early-developing characters, and among 20 QTLs affecting the late-developing characters. For the early-developing skull characters, epistatic effects were predominantly of the additive-by-dominance or dominance-by-additive type, and made only a small contribution to the total variance (they explained an additional 2% of the variance beyond that for the single-locus contributions). For the late-developing skull characters, epistatic effects were predominantly of the dominance-by-dominance type, and explained on average an additional 9% of the total variance beyond that contributed by single-locus effects. The majority of these epistatic effects were restricted to one character. The patterns of epistatic pleiotropy that did occur produced only minor alterations of within-group correlations of characters and did not substantially alter their overall mean level or degree of integration. There also was only limited evidence for differential epistasis in which one QTL suppressed the pleiotropic effects of other QTLs that influenced characters in either the early- or the late-developing skull groups.

23.5

DEVELOPMENTAL INSTABILITY OF THE SKULL IN ANEUPLOIDY

[1]**Joan T. Richtsmeier,** [1]Jennifer M. Leszl, [1]Cheryl A. Hill, [1]Jaime L. Budd,
[2]Roger R. Reeves

[1]*The Pennsylvania State University, 409 Carpenter Bldg, University Park, PA 16802, USA*
[2]*Johns Hopkins University School of Medicine, 725 N. Wolfe St., Baltimore, MD, 21205* USA

Down syndrome (DS), caused by trisomy of human Chromosome 21 (Chr21), causes a spectrum of complex phenotypes. Two hypotheses proposed to explain DS phenotypes include: 1) “developmental instability” hypothesis that holds that the correct balance of gene expression in pathways regulating development is disrupted by dosage imbalance of the genes on Chr21; and 2) “gene dosage effects” hypothesis that asserts that dosage imbalance of specific genes from Chr21 are responsible for specific DS traits. Ts65Dn mice have segmental trisomy for the distal end of mouse Chr16 that corresponds to a portion of Chr21 containing 118 of the 225 genes in the Chr21 gene catalogue. The Ts65Dn genetic insult corresponds to that of humans with segmental trisomy 21 and adult Ts65Dn skulls show dysmorphologies paralleling skull dysmorphology in DS. Landmark coordinate data collected from adult mouse skulls and from micro-CT images of newborn (P0) mice were combined with new landmark-based morphological integration (MI) and fluctuating asymmetry (FA) methods to assess the developmental instability hypothesis. When compared to euploid littermates, P0 aneuploid crania and mandibles show subtle decreases in MI local to the occiput. FA is significantly increased in P0 aneuploid mice local to the cranial base and frontonasal. Analysis of adult mice indicates that MI is increased on the frontonasal region and mandible of aneuploid individuals, areas that showed local patterns of dysmorphology in aneuploid adults. FA is comparable between adult euploid and aneuploid mice although the euploid sample shows some localized areas of significantly increased FA. Significant differences in MI and FA between euploid and aneuploid Ts65Dn mice are highly localized. The correspondence between areas of aneuploid skull dysmorphology and those of increased correlation among traits suggests that constraints on phenotypic outcomes produced by patterns of covariation among traits should be considered in further hypotheses regarding the development of phenotypes in DS.

23.6

THE USE OF MOUSE MUTANT MODELS FOR UNDERSTANDING CANALIZATION AND DEVELOPMENTAL STABILITY

[1]Benedikt Hallgrimsson, [1]Katherine Willmore, [1]Michelle Dymond

[1]University of Calgary, 3330 Hospital Dr. NW, Calgary, AB Canada, T2N 4N1

[2]Dalhousie University, 1355 Oxford Street, Halifax, NS, Canada, B3H 4J1

Variability, or the propensity of organisms for exhibiting phenotypic variation in response to genetic and environmental effects, is an emergent property of complex developmental systems. Although both theory and evidence suggest that variability exhibited by developmental systems can be modulated by genetic and environmental factors, very little is known about what factors affect variability and the mechanisms that underlie such effects. In this paper, we report on a research program that aims to identify the classes of genetic perturbations that affect developmental stability (DS) and canalization, two components of variability, in mouse skeletal development. We compare the effects of mutations that produce disparate kinds of developmental changes in the same anatomical structures, focusing on limb and craniofacial skeletal morphology. We compare the effects of a collagen mutation (Col1a2) that mimic osteogenesis imperfecta with a null mutation in the growth hormone releasing hormone receptor (Ghrhr) that affects postnatal skeletal growth and find that while the collagen mutation has no effect on variability in skeletal structures (despite profoundly deleterious phenotypic effects), a small but significant effect on DS and canalization is observed for the Ghrhr null mice. We report on ongoing studies of the effects of mutations which perturb craniofacial development on variability of craniofacial morphology in mice. The studies completed so far suggest that the reduction in FA and canalization, if present, is confined to the anatomical region in which size and shape are most immediately affected by the mutation. We hypothesize that a factor which influences skeletal growth is more likely to result in an increase in variability than a factor which affects bone structure and metabolism. This finding casts doubt on the usefulness of FA as an indicator of mate "quality" since many mutations which significantly reduce fitness may have no effect on variability.

23.7

MORPHOLOGICAL VARIABILITY IN MANDIBLE SHAPE OF WOOD MICE (*APODEMUS*): LATITUDINAL GRADIENTS AS ADAPTIVE TREND?

[1]Sabrina Renaud, [2]Johan R. Michaux

[1]UMR5125, CNRS - UCB Lyon 1, Bat G/ode, 2 rue R. Dubois, Campus de la Doua, 69622 Villeurbanne, France

[2]Institut de Zoologie, 4020 Li?ge, Belgique

Different factors may pattern the natural morphological variability. We investigated the size and shape variability of the mandible of the European wood mouse (*Apodemus sylvaticus*), using a Fourier analysis of the outline of the mandible. This model was chosen because an important genetic structure within this species has been evidenced by previous studies; insular populations may locally diverge from their mainland relatives, and the wood mouse covers an important latitudinal gradient, allowing for a test of the relative importance of these factors. This analysis showed that within the European wood mouse, a strong latitudinal gradient in mandible shape overrides the influence of insularity and genetic structure. Yet, random morphological divergence in insular conditions can be identified as a secondary feature of shape differentiation. These results were compared with those on two Asiatic species of wood mice, *A. argenteus* and *A. speciosus*. A similar latitudinal gradient in mandible shape was found in the different species, associated with a dorso-ventral expansion at the coronoid and angular processes towards Southern populations. We suggest that this may be an adaptive response to a shift in the feeding habits in populations confronted to different seasonal variations and average annual diet and behaviour.

23.8P

DOSAGE EFFECT OF STANDARD GENE ARRANGEMENTS ON WING SHAPE AND SIZE IN *DROSOPHILA SUBOBSCURA*

[1]P. Fernandez Iriarte, [1]W. Caspedes, [2]J. Balanyi, [2]L. Serra, [1]A. Fontdevila, [1]M. Santos

[1]Grup de Biologia Evolutiva, Departament de Genetica i de Microbiologia, Universitat Autonoma de Barcelona, 08193 Bellaterra (Barcelona), Spain

[2]Grup de Biologia Evolutiva, Departament de Genetica, Universitat de Barcelona, Diagonal 645, 08071 Barcelona, Spain

Latitudinal clines in chromosomal arrangement frequencies have been observed in natural populations of *Drosophila subobscura*, with the so-called standard arrangements in the five (out of six considering the dot chromosome) acrocentric chromosomes increasing in frequency with latitude. Likewise, parallel body size (measured as wing length) genetic clines as the long-standing ones in native European populations appeared in New World populations too, although it took about 20 years after the colonization for the clines to build up. However, the increase in wing length with latitude in the European cline was associated with a relative lengthening of the basal portion of the longitudinal vein IV, whereas the increase in North America was associated with an increase in the distal portion of the same vein. Differences in the position of the posterior cross vein have been explained as likely due to drift around an optimum. We have developed a set of three replicated *D. subobscura* thermal selection stocks to study the short and long term effects of temperature on genetic variation. Log-linear analyses performed on samples from the populations after one year of selection (27 generations of divergence at most) show a significant and consistent effect of temperature on standard-chromosome dosage effects but, unexpectedly according to the latitudinal clines, the average standard dosages are higher at warmer temperatures. Furthermore, there is a strong relationship between the standard dosage and the relative lengths of the two partial segments that define total wing length of vein IV, suggesting that the North America cline for wing shape may be a correlated result of selection acting on a particular genetic composition of founding populations rather than pure chance.

23.9P

SWIFT LABORATORY THERMAL EVOLUTION OF WING SHAPE (BUT NOT SIZE) IN *DROSOPHILA SUBOBSCURA*

[1]M. Santos, [1]P. Fernandez Iriarte, [1]W. Caspedes, [1]A. Fontdevila, [2]J.Balanyi, [2]L. Serra

[1]*Universitat Autonoma de Barcelona, 08193 Bellaterra (Barcelona), Spain*

[2]*Universitat de Barcelona, Diagonal 645, 08071 Barcelona, Spain*

Latitudinal clinal variation in wing size and shape has evolved in North American populations of *Drosophila subobscura* within about 20 years since colonization. While the size cline is consistent to that found in original European populations (and globally in other Drosophila species), different parts of the wing have evolved on the two continents. This clearly suggests that 'chance and necessity' are simultaneously playing their roles in the process of adaptation. We report here rapid and consistent thermal evolution of wing shape (but not size) that apparently is at odds with that suggestion. Three replicated populations of *D. subobscura* were kept at each of three temperatures (13?C, 18?C and 22?C) for one year and have diverged for 27 generations at most. We used the methods of geometric morphometrics to study wing shape variation in both females and males from the thermal stocks, and rates of genetic divergence for wing shape were found to be as fast or even faster than those previously estimated for wing size on a continental scale. These shape changes did not follow a neat linear trend with temperature, and are associated to localized shifts of particular landmarks with some differences between sexes. The possibility that changes in gene arrangement frequencies as a response to temperature underlie the correlated changes in wing shape because of gene-inversion linkage disequilibria is discussed.

23.10P

VARIANCE COMPONENTS AND DEVELOPMENTAL STABILITY IN RHESUS MACAQUE SKULLS

Katherine E. Willmore, Benedikt Hallgrimsson

University of Calgary, Health Sciences Center, 3330 Hospital Drive NW, Calgary, Alberta, Canada

Canalization and developmental stability have traditionally been considered two separate phenomena governed by different processes. Canalization is thought to buffer development against genetic and macro-environmental perturbations, while developmental stability buffers against developmental noise or micro-environmental disruptions. Recent studies however, have shown that there may be an association between the two properties and that this stringent demarcation between the two phenomena may be arbitrary. The aim of this study was to investigate the potential relationship between developmental stability and canalization using measures of fluctuating asymmetry (FA) and environmental variance from adult macaque skulls from Cayo Santiago. Using the traditional definitions, increased FA would indicate increased susceptibility to micro-environmental noise, and increased environmental variance would suggest an increased susceptibility to macro-environmental noise. We hypothesize that developmental stability and canalization are related and therefore we expect to see a positive correlation between FA and environmental variance. The sample consists of 228 skulls and was chosen based on known matrilineal relationships. 3 dimensional data were collected from 34 bilateral skull landmarks. FA and heritability were calculated from procrustes coordinate data for each of these landmarks. FA was calculated using Palmer and Strobeck's (1994, 2002) two-way mixed model ANOVA, and heritability was estimated from mother-offspring, half sibling, grandmother-offspring and aunt-offspring correlations. Environmental variance was calculated for each of these relationships by the equation 1-H2 and was scaled to the total phenotypic variance. FA was significant for 68 of 102 coordinates. However, regressions between the FA and environmental variance for these coordinates were insignificant. Based on this data, we must reject our hypothesis that the processes governing canalization and developmental stability are associated. We plan on investigating the association between the two phenomena further using transgenic mouse models for which the genetic background can be accounted and both environmental and genetic perturbations can be experimentally controlled.

Symposium 24

Social plasticity

Organisers: Jürgen Heinze & Patrizia d'Ettorre

Roger Stevens Lecture Theatre 21

14.00 – 14.30	**Bourke, A.** Social plasticity and its consequences in social insects
14.30 – 15.00	**O'Riain, J. M.** Naked mole-rats - pushing the limits of mammalian plasticity
15.00 – 15.20	**Korb, J.** Solitary spotted hyenas, *Crocuta crocuta*: Social plasticity in a typical group living carnivore and its potential causes
15.20 – 16.00	**Tea**
16.00 – 16.20	**Sundström, L.** Phenotypic plasticity in facultatively polygyne ants
16.20 – 16.40	**Foitzik, S.** Ecology of *Leptothorax* ants: impact of food, nest sites and social parasites
16.40 – 17.00	**Faurie, C.** Fights and the evolution of handedness: a cross-cultural study.
17.00 – 17.20	**Salonen, A.** Spatial and temporal distribution of food - The effect on aggressive behaviour in European graylin (Thymallus: Salmonidae)

Invited talks

24.1

SOCIAL PLASTICITY AND ITS CONSEQUENCES IN SOCIAL INSECTS

Andrew Bourke

Institute of Zoology, Zoological Society of London, Regent's Park, London, NW1 4RY, UK

Many social insects exhibit within-species variation in their social structure. Although this may in some cases be associated with genetic polymorphisms, in most it is assumed to be the result of a flexible response to local environmental or demographic conditions. Whatever the basis of this variation, its existence has important consequences for other social traits and for patterns of further social evolution. I illustrate this with two case studies. One is the ant *Leptothorax acervorum*, whose populations include colonies headed by single queens and colonies headed by multiple queens (facultative polygyny). The other is the bumble bee *Bombus terrestris*, which exhibits a between-colony polymorphism in the sex ratio and in the timing of production of sexuals that, interestingly, is not associated with differences in the social or relatedness structure of colonies. Why social variation among social insects occurs in some cases at the between- colony level, in others at the between-population level, and in other cases again at the between-species level, is not well understood. I discuss some of the factors that might maintain social polymorphisms within species, including some such as the frequency-dependent success of different social types that are likely to have been operative at the origin of eusociality.

24.2

NAKED MOLE-RATS - PUSHING THE LIMITS OF MAMMALIAN PLASTICITY

M. Justin O'Riain

Zoology Department, University of Cape Town, Rondebosch, 7700, South Africa.

Individuals within a colony of naked mole-rats exhibit an extraordinary degree of behavioural and morphological variation, despite their limited genetic differences. Indeed the species name, *Heterocephalus glaber*, refers not only to their nakedness (glaber) but the obvious differences that are apparent in the shape of colony members' heads (Heterocephalus). Long-term ontogenetic studies have helped to elucidate how these differences arise and their adaptive significance. Perhaps most striking is the evolution of a mammalian equivalent of the morphologically distinct queens, typical of many eusocial insect societies. These mole-rat queens arise from the ranks of non-breeders and following the onset of reproduction undergo remarkable morphological, physiological and behavioural changes. X-rays have revealed that incipient queens experience a growth spurt (despite being adults), with disproportionate lengthening of their lumbar vertebrae. The result is a greatly enlarged abdominal region capable of supporting significantly larger litter sizes (up to 28 pups). Differences amongst the non-breeders are more subtle, with the more physically robust individuals engaging in a higher proportion of defensive activities. These differences are continuous and largely dictated to by the relative age of individuals with older siblings apparently suppressing the growth of their younger kin. Only one exception to this continuum is apparent and that is the rare dispersive morph. These individuals are characterised by large deposits of fat, high circulating levels of luteinising hormone and show a highly uncharacteristic preference for foreign conspecifics. Together these results present a picture of striking plasticity and I propose to discuss how this facilitates our understanding of the processes underlying the evolution of sociality.

Contributed talks

24.3

SOLITARY SPOTTED HYENAS, *CROCUTA CROCUTA*: SOCIAL PLASTICITY IN A TYPICAL GROUP LIVING CARNIVORE AND ITS POTENTIAL CAUSES

Judith Korb

University of Regensburg, Biology I, Universitaetsstr., 93040 Regensburg, Germany

Spotted hyenas, *Crocuta crocuta*, have been intensively studied and are known to live in social groups (clans). Here data will be presented that show for the first time that spotted hyenas can also live solitarily, thus illustrating the large degree of social plasticity of a typical social carnivore. It was tested whether this contrast in social organisation can be explained by differences in food availability by comparison of the prey spectra. In areas in eastern and southern Africa spotted hyenas live in clans of up to 80 individuals. By contrast in the Comoé National Park (CNP) in Ivory Coast (West Africa) spotted hyenas did not form clans, but lived solitarily. While spotted hyenas mainly prey on large and medium sized mammals (e.g. wildebeest, zebra, impala) in the former areas, the prey spectrum in the CNP consisted predominately of small mammals (cane rat: 25 %, Senegal kob: 20 %). Large mammals that are hunted in groups in other areas, occurred only at low densities in the CNP (< 1 animal / km2). In accordance with game theory models on group foraging, this lack of large prey can explain the solitary live of spotted hyenas in the CNP.

24.4

PHENOTYPIC PLASTICITY IN FACULTATIVELY POLYGYNE ANTS

[1]**Liselotte Sundström,** [2]Christine Johnson, [3]Vanya Emelianoff, [2]Johan Billen,

[1]*University of Helsinki, Department of Ecology and Systematics, P.O.Box 65, FIN-00014 Helsinki*

[2]*Catholic University of Leuven, Department of Biology, Naamsestraat 59, B-3000 Leuven*

[3]*Ecole Normale Superieure, 45 rue d'Ulm, 75005, Paris*

In several species of ants the number of reproductively active queens may vary extensively, such that colonies of some species contain only one queen (monogyny), whereas colonies of other species regularly contain several queens (polygyny). Such variation in queen numbers may also be found within species. Comparisons between closely related single-queen and multi-queen species have revealed a multitude of differences in dispersal tendencies, reproductive behaviour, physiology and morphology. Similar, but less pronounced, variation has been demonstrated in facultatively polygyne species. This begs the question whether the observed differences have arisen following adaptation to divergent ecological conditions, or reflect phenotypically plastic traits. In the former case the expectation is that young queens differ with respect to size, condition and behaviour regardless of social environment. In the latter case no consistent differences in morphology, histology or cuticular chemistry would be expected and young queens raised in similar social environments would converge in these traits. Here we compare reproductive choices, morphology, histology and cuticular chemistry of females originating from mono- and polygyne populations of the facultatively polygyne ant *Formica truncorum*. To assess prospects of independent colony founding, we also analyse maturation patterns and survival in females exposed to different social environments in a cross-fostering experiment.

24.5

ECOLOGY OF *LEPTOTHORAX* ANTS: IMPACT OF FOOD, NEST SITES AND SOCIAL PARASITES

[1]**Susanne Foitzik,** [2]Joan M. Herbers

[1]LS Biologie I, Universität Regensburg, 93040 Regensburg, Germany

[2]College of Biological Sciences, Ohio State University, Columbus, Ohio 43210, USA

For a long time, studies on social insects have been strongly influenced by theories of inclusive fitness, sex ratio and reproductive skew. Tests of these models have been facilitated by the development of powerful genetic markers and consequently a large literature evaluating intracolonial relatedness is now available. By contrast, evaluation of model predictions about ecological parameters has been slower because they are difficult to measure and can interact with the social structure of colonies. We demonstrate in a long-term field manipulation strong reactions of *Leptothorax longispinosus* ant colonies to food and nest site field supplementation. However, responses varied over small geographic scales and the two ecological factors interacted with the presence of the social parasite, *Protomognathus americanus*. We conducted a 2x2 experiment at three sites and found that areas, which were less than 100m apart, reacted very differently to the same treatments. Sites differed in the rate of polygyny, intranest relatedness, colony size, productivity and sexual investment, and these differences were associated with the presence of the slavemakers and the local availability of nest sites. Nest site supplementation had a strong effect only at the site with the highest parasite prevalence, influencing density and investment patterns of colonies. *L. longispinosus* ants in the least parasitized area were strongly affected by both food and nest site supplementation. There, food supplementation led to a decrease in the number of queens per colony and consequently to an increase in intranest relatedness, while colonies in nest site supplemented areas raised fewer males and produced a female biased allocation ratio. By contrast, at another site, food supplementation induced an absolute and relative higher investment in males. We conclude that ecological factors influencing social organization in insect societies cannot be studied in isolation, because the interaction among factors produces far richer responses than any one variable.

24.6

FIGHTS AND THE EVOLUTION OF HANDEDNESS: A CROSS-CULTURAL STUDY

Charlotte Faurie, Michel Raymond

Génétique de l'Adaptation - ISEM – Institut des Sciences de l'Evolution - CC065 - Place E. Bataillon - F- 34095 Montpellier cedex 5 - France

A polymorphism of handedness exists in all human populations so far investigated, at least since the Palaeolithic. Handedness is a heritable trait, with a significant genetic contribution. A possible evolutionary explanation for the higher prevalence of right-handers is the association of left-handedness with some deleterious traits, shown by many authors. However, some sort of balancing selection must be acting, to maintain the polymorphism. Thus, some advantages of left-handers have to be found. The polymorphism of handedness is often viewed as a mere consequence of indirect selection. The only explanation proposed so far for a direct selective cause of this polymorphism is the fighting hypothesis: As left- handers are less frequent, one is more likely to be confronted with a right-handed opponent. Left-handers thus get the benefit of being rare. This frequency-dependent superiority of left-handers in fights would confer them fitness advantages, directly and indirectly. Not only their survival would be enhanced, but also their social status and reproductive success, as real or ritualised fights have important consequences on social status. The fighting hypothesis is supported by the study of interactive sports in western societies. To test further the fighting hypothesis, we use a cross-cultural comparison. As levels of male/male aggression vary cross- culturally, we expect to observe matching cross-cultural variation in the frequency of left-handedness. The data presented, collected in traditional societies, are consistent with this prediction of the fighting hypothesis.

24.7

SPATIAL AND TEMPORAL DISTRIBUTION OF FOOD - THE EFFECT ON AGGRESSIVE BEHAVIOUR IN EUROPEAN GRAYLING (THYMALLUS:SALMONIDAE)

[1]**A. Salonen**, [2]N. Peuhkuri

[1]*University of Helsinki, Department of Ecology and Systematics, Po Box 65, Fin-00014*

[2]*Finnish Game and Fisheries Research Institute, Fin-48100 Kotka*

We have some evidence that aggressive behaviour of European grayling differs between lake and river populations. In these two habitats spatial and temporal distribution of food is presumably different, which may have effects on the profitability of defending food. In the river, fry feed in current where food floats from upstream being spatially and temporally predictable. The predictability of food may promote aggressive defending of occupied feeding area. In lakes, fish exploit larger grounds to find both spatially and temporally less predictable food patches and unpredictable existence of food may lead to lower level of aggressions in lake populations of European grayling. I studied the effect of spatial and temporal food distribution on agonistic behaviour in young-of-the-year grayling. Fish from lake and river populations were reared in different feeding conditions 1) continuous and 2) periodic feeding in the upstream and 3) periodic feeding in spatially unpredictable locations. Aggressiveness of fish was experimentally tested and distribution of food in the rearing environment was found to affect aggressive behaviour of fry. Aggressiveness of individuals was highest when food was offered periodically to spatially predictable location. This indicates that spatial predictability of food has an increasing effect on aggressive behaviour of European grayling and that predictability of food existence may be one factor causing the difference in the aggressive behaviour between lake and river populations.

Posters

24.8P

POPULATION GENETIC STRUCTURE OF *FORMICA SELYSI*, AN ANT WITH VARIABLE SOCIAL STRUCTURE

M. Chapuisat, S. Bocherens, H. Rosset

University of Lausanne, Institute of Ecology, Biology Building, 1015 Lausanne, Switzerland

Variation in the social structure of ants alters the genetic structure of colonies, which in turn affects patterns of kin-selected conflict and cooperation. Hence, studying the causes, correlates and dynamics of variation in the number of queens per colony is important to gain a better understanding of social evolution. Theory suggests that shifts from single-queen to multiple-queen colonies are often associated with other changes in the breeding system, such as higher queen turnover, more local mating, and restricted dispersal. These changes may restrict gene flow between the two types of colonies and ultimately lead to sympatric speciation. We performed a detailed microsatellite analysis of a large population of the ant *Formica selysi*, which revealed extensive variation in social structure, with 71 colonies being headed by a single queen and 41 by multiple queens. This social polymorphism appeared stable over time, as little change in the number of queens per colony was detected over a five year period. Surprisingly, both single-queen and multiple-queen colonies showed low queen turnover, small but significant levels of inbreeding, and very little genetic structuring above the nest level, with no isolation by distance. These similarities in the breeding systems were associated with a complete lack of genetic differentiation between the two social types, which provides no support to the hypothesis that change in queen number leads to restricted gene flow between social forms and promotes speciation. Together, these data suggest that diversifying selection maintains a stable social polymorphism within this panmictic population.

24.9P

SOCIAL PLASTICITY IN A TEMPORARY SOCIAL PARASITE

K.H. Falk, J. Gadau, J. Liebig, B. Hoelldobler

Department of Sociobiology and Behavioural Physiology, University of Wuerzburg, Am Hubland, 97074 Wuerzburg, Germany

The Palaearctic ant *Lasius fuliginosus* is a temporary social parasite of congeneric species. The young newly mated queen invades the nest of a host and tries to usurp the colony. After the death of the host queen the colony becomes a mixture of the two species with an increasing number of *L. fuliginosus* workers. Subsequently this results in a monospecific and monogynous (i.e. containing one single queen) colony. Mature colonies of *L. fuliginosus*, however, are reported to have occasionally more than one reproductive queen. This might be due to different mechanisms: Young fertilized queens may not only invade colonies of a different but also the same species (intraspecific social parasitism). On the other hand *L. fuliginosus* colonies might be prone to adopt newly mated queens especially own offspring - to increase the longevity or the genetic diversity of the colony, for instance. In this study we investigated the social structure of colonies in a German *L. fuliginosus* population using microsatellites and mtDNA as genetic markers. In 2 out of 19 colonies we found more than one reproductive queen. We also examined if these colonies were simply polygynous (i.e. multiple egg-laying queens per colony) or oligogynous (i.e. multiple egg-laying queens spatially separated and mutually intolerant) and, moreover, if the participating queens were related to each other. Both polygyny and oligogyny may be followed by colony budding which results in new autonomous and monogynous colonies. Therefore we also tested if neighboured colonies formed matrilineal clusters. If budding occurs it might serve as an alternative founding strategy to avoid the costs of interspecific social parasitism.

Symposium 25

Genome size, cell size and scaling metabolic rate: a cytogenetic approach to life history evolution

Organisers: Marek Konarzewski & Jan Kozlowski

Roger Stevens Lecture Theatre 22

14.00 – 14.30	**Gregory, T. R.** Aves versus Amphibia: Why organismal biology matters in genome size evolution (and vice versa)
14.30 – 15.00	**Morand, S.** Genome size and life history traits in primates
15.00 – 15.20	**Kozlowski, J.** Cell size as a link between junk DNA and scaling of metabolic rate
15.20 – 16.00	**Tea**
16.00 – 16.20	**Konarzewski, M.** Genome size and scaling of metabolic rate in homeotherms
16.20 – 16.40	**Olmo, E.** Reptiles: a group of transition in the evolution of genome size and nucleotypic effect
16.40 – 17.00	**Glazier, D. S.** Evolution of differences in metabolic scaling in pelagic versus non-pelagic animals

Invited talks

25.1

AVES VERSUS AMPHIBIA: WHY ORGANISMAL BIOLOGY MATTERS IN GENOME SIZE EVOLUTION (AND VICE VERSA)

T. Ryan Gregory

Division of Invertebrate Zoology, American Museum of Natural History, New York, NY, USA.

The evolution of genome size is a complex puzzle that has defied one-dimensional explanations for over half a century. While important links have been identified between genome size and various organismal characteristics, these are not always universally applicable. As such, no one correlate – be it metabolic, developmental, or otherwise – will account for all variation in genome size. This talk compares and contrasts the impacts of genome size variation in birds and amphibians. Metabolic constraints are shown to be important in the former but largely irrelevant in the latter, while the reverse is true of developmental parameters. For this reason, it is important to consider organismal biology in questions of genome size and vice versa.

25.2

GENOME SIZE AND LIFE HISTORY TRAITS IN PRIMATES

Serge Morand

The Centre for Biology and Management of Populations, Montferrier sur Lez Cédex , France

Genome size (C, the DNA content of the cell) varies widely among eukaryotes, increasing through duplication or insertion of transposable elements and decreasing through deletions and DNA repair mechanisms. The consequences of variation in C, thus potential selection on genome size, are not well understood. Here, we investigate relationships between genome size and life history attributes potentially related to fitness, including body mass, brain mass, gestation time, age at sexual maturity, and longevity, in 42 species of primates. Using multivariate and phylogenetically controlled analyses, we show that genome size is unrelated to any of these traits. Thus, although genome size exhibits phylogenetic conservatism, its evolution does not appear to be correlated with changes in life history traits. The fitness consequences of variation in genome size are not elucidated by comparative analysis of variation in fitness related traits among species.

Contributed talks

25.3

CELL SIZE AS A LINK BETWEEN JUNK DNA AND SCALING OF METABOLIC RATE

J. Kozlowski, M. Konarzewski, A. T. Gawelczyk

Institute of Environmental Sciences, Jagiellonian University, Krakow, Poland and University of Bialystok, Institute of Biology, Bialystok, Poland

Accumulation of junk DNA and therefore genome size (C-value) may be under strong selection toward increase of body size accompanied by low metabolic costs. C-value directly affects cell size and specific metabolic rate indirectly. Body size can enlarge through increase of cell size and/or cell number, with small cells having higher metabolic rates. We argue that interspecific allometries of metabolic rate for broad taxons are by-products of its allometric scaling within narrow taxonomic groups. Values of scaling exponents depend on evolutionary diversification of C-value, which underlines the participation of cell size and cell number in body size optimization. This optimization reduces the slopes of interspecific allometries because the lifetime reproduction of species with a greater difference between resource acquisition and metabolic rates is maximized at larger body sizes. In a sister paper (Konarzewski and Kozlowski) these predictions are tested on birds and mammals.

25.4

GENOME SIZE AND SCALING OF METABOLIC RATE IN HOMEOTHERMS

Marek Konarzewski, Jan Kozlowski

University of Bialystok, Institute of Biology, Bialystok, Poland and Institute of Environmental Sciences,Jagiellonian University, Krakow, Poland

In a sister, theoretical paper (Kozlowski, Konarzewski and Gawelczyk) we concluded that allometric scaling of basal metabolic rate (BMR) with body size is in part determined by genome size (C-value). This is because values of metabolic scaling exponents depend on evolutionary diversification of C-value, which underlines the participation of cell metabolism in body size optimization. We predicted that within narrow taxonomic groups low values of slopes of whole-body metabolic scaling should be associated with a steep scaling of C-value with body size. Conversely, lower values of allometric slopes of C-value with body size should be associated with steeper allometric slopes of metabolic rates. Thus, there should exist a negative correlation between scaling of BMR and scaling of C-value. To test this prediction we extracted literature data on BMR, body mass and C-value of mammals and birds representing 6 and 8 orders, respectively. The analysis of covariance revealed a significant heterogeneity of allometric slopes of BMR and C-value both, in mammals and birds. As we predicted, the correlation between allometric exponents of BMR and C-value were negative and statistically significant among mammalian and avian orders.

25.5

REPTILES: A GROUP OF TRANSITION IN THE EVOLUTION OF GENOME SIZE AND NUCLEOTYPIC EFFECT

E. Olmo

Polytechnical University of the Marche, Institute of Biology and Genetics, Ancona, Italy

Reptilian genome and cell sizes are comparatively small and fairly similar to those of mammals. The range of size variation of their genome is believed to have undergone very few modifications during evolution. These changes seem to have been affected by two main factors. – The nucleotpic effect of genome size on metabolism, whereby small genomes and cells are required for a high cellular metabolism. Reptiles are indeed the first terrestrial vertebrates with some capacity for thermoregulation and are able to reach and maintain much higher temperatures than the environment also via metabolic production of heat. The maintenance of fairly high temperatures (30°-33°C) is essential for these organisms in terms of both embryo development and adult life. - As regards genome size, despite largely overlapping ranges of DNA values, Chelonians exhibit, on average, larger genome sizes than Squamates. These two groups also differ in terms of certain compositional features of the genome, in their chromosome banding patterns and in the level of deletions and recombinations (which is higher in Squamates). Chelonians thus seem to possess a genome structure that may have favoured the accumulation and preservation of repetitive DNA sequences and consequently an increase in genome size.

25.6

EVOLUTION OF DIFFERENCES IN METABOLIC SCALING IN PELAGIC VERSUS NON-PELAGIC ANIMALS.

Douglas S. Glazier

Juniata College, Brumbaugh Science Center, Huntingdon, PA, USA

Recently, several theoretical models have been constructed to explain the "3/4-power scaling law" of metabolic rate. Many investigators have assumed that the 3/4 power law is universally applicable, but recent empirical investigations have shown that many exceptions exist, both within and among animal species. My survey of animals reveals four major types of intraspecific metabolic scaling with body mass [based on the power function $R = aM^b$, where R is respiration (metabolic) rate, a is a constant, M is body mass, and b is the scaling exponent]: Type I: linear, negatively allometric ($b < 1$); Type II: linear, isometric ($b = 1$); Type III: nonlinear, ontogenetic shift from isometric ($b = 1$), or nearly isometric, to negatively allometric ($b < 1$); and Type IV: nonlinear, ontogenetic shift from positively allometric ($b > 1$) to one or two later phases of negative allometry ($b < 1$). Here I focus on the Type II metabolic scaling shown by pelagic species in five different phyla with very different body designs. This remarkable case of convergent evolution is further supported by comparing the metabolic scaling of pelagic and non-pelagic species within specific phyla (e.g., Cnidaria and Chordata), and of planktonic larvae and benthic adults in the same species. Since pelagic animals are exposed to high levels of predation and are generally short-lived, they appear to be subject to natural selection favoring rapid rates of growth and reproduction. Rapid rates of continuous production may in turn require high levels of metabolism at all stages of development and body size, thus resulting in isometric metabolic scaling. I conclude that the scaling of metabolism is not the simple result of physical law, but rather appears to be the more complex result of diverse adaptations evolved in the context of both physiological and ecological constraints.

Posters - none

Symposium 26

Theoretical and empirical aspects of the evolution of diversity: speciation, species discovery, and inventory

Organiser: Douglas Causey

Roger Stevens Lecture Theatre 20

09.50 – 10.20	**Causey, D.** How to quantify biodiversity
10.20 – 11.00	**Coffee**
11.00 – 11.30	**Hey, J.** Understanding and confronting species uncertainty in biology and conservation
11.30 – 12.00	**Krishtalka, L.** Modelling evolutionary phenomena using biodiversity informatics
12.00 – 12.20	**Gomez, A.** The evolution of biodiversity: what can we learn from cryptic species?
12.20 – 12.40	**Tautz, D.** The use of DNA taxonomy for species inventories
12.40 – 14.00	**Lunch**
14.00 – 14.20	**Saetre, G-P.** Speciation as a positive feedback loop between pre- and postzygotic barriers to gene flow
14.20 – 14.40	**Weingartner, E. L.** Speciation processes and host plant utilization in Polygonia butterflies
14.40 – 15.00	**Gavrilets, S.** On models of sympatric speciation
15.00 – 15. 20	**Drossel, B.** Speciation and cospeciation in quantitative genetic models
15.20 – 16.00	**Tea**
16.00 – 16.20	**Cohen, D.** Modeling evolutionary and ecological consequences of selection in heterogeneous environments
16.20 – 16.40	**Burzynski, A.** Evolution of mitochondrial inheritance in mussels from Baltic Sea
16.40 – 17. 00	**Barraclough, T. G.** Diversification in sexuals and asexuals
17.00 – 17.20	**Grande, C.** Molecular systematics of Euthyneura (Mollusca: Gastropoda)

Invited talks

26.1

HOW TO QUANTIFY BIODIVERSITY

Douglas Causey

Museum of Comparative Zoology, Harvard University, Cambridge, MA

New approaches to biodiversity inventory, new developments in species concepts, and innovative technology are enabling dramatic new directions in species discovery, identification, and classification. Traditional methods are clearly inadequate for the task, in terms of what needs to be done and in terms of the increasing rate of habitat destruction and species loss. I explore several promising new directions in inventory, molecular-based species discovery, and quantitative natural history as a means of understanding where the future of biodiversity study may be headed.

26.2

UNDERSTANDING AND CONFRONTING SPECIES UNCERTAINTY IN BIOLOGY AND CONSERVATION

Jody Hey

Rutgers University

Biologists who endure the species problem can benefit from a synthesis in which individual taxonomic species are used as hypotheses of evolutionary entities. Two sources of species uncertainty are revealed, one that is a semantic confusion, and a second that is caused by the inherent vagueness of the ways that evolutionary entities exist. The former can be dispelled with careful communication, whereas the latter is a conventional scientific uncertainty that can only be mitigated by research. This scientific uncertainty cannot be 'solved' or stamped out, but neither need it be ignored or feared.

26.3

MODELING EVOLUTIONARY PHENOMENA USING BIODIVERSITY INFORMATICS

Leonard Krishtalka

Department of Ecology and Evolutionary Biology, The University of Kansas, Dyche Hall, 1345 Jayhawk Blvd, Lawrence, KS 66045-7561

The hallmark of human evolution has been information management, from rock carvings to the Web. Today, information technology is enabling research on the grand challenges in science for the 21st Century in cosmological systems, Earth systems and human systems. One example is the grand challenge of understanding Earth's biological diversity and how it shapes the global environmental systems on which all of life depends. Using biodiversity informatics, which combines information technology with computational engineering, researchers at the University of Kansas Biodiversity Research Center are networking and integrating biological data from millions of specimens of animals and plants in the world's natural history institutions via the web with data and analytical tools from other disciplines for analysis and predictive modeling of evolutionary and biodiversity phenomena. The enormous bank of biological information contained in the world's natural history museum collections--approximately 3 billion specimens of animals and plants--represents 300 years of the biological exploration of the planet, but lay largely untapped. Now it is being deployed to analyze and predict phenomena such as the ecological niches, distributions and divergence of species of animals and plants, the potential spread and threat of invasive species, pest species, emerging diseases and bioterrorism agents, and the impact of global change on biodiversity worldwide.

Contributed talks

26.4

THE EVOLUTION OF BIODIVERSITY: WHAT CAN WE LEARN FROM CRYPTIC SPECIES?

Africa Gomez, Gary R. Carvalho, David H. Lunt,

Department of Biological Sciences, University of Hull, Hull, HU6 7RX, U.K.

The striking discrepancy observed between genetic and phenotypic diversification is partly due to the occurrence of cryptic species. Cryptic or sibling species, lacking conspicuous diagnostic morphological characters, but identifiable from other biologically relevant features, are increasingly being recognised through the cost-effective use of PCR-based molecular techniques. The widespread presence of cryptic species is responsible for the underestimation of the biodiversity in many animal phyla. The discovery of cryptic species has increased the perceived biodiversity of the Earth ecosystems, but most importantly, it has provided a window of opportunity to understand ecology and evolution in a wider context. We discuss here that some common life-history traits and evolutionary features of cryptic species may help us to reconsider the main factors involved in population diversification and speciation. We illustrate these ideas with two cosmopolitan taxa that we have investigated recently: the rotifer *Brachionus plicatilis*, which inhabits salt water lakes and ponds, and the marine littoral bryozoan *Celleporella hyalina*. Rotifer and bryozoans have complex life cycles showing certain parallels: both alternate a clonal and a sexual phase, and the dispersive passive stage is formed sexually (resting egg and planktonic larvae respectively). Nucleotide sequence information on mitochondrial and nuclear DNA showed that both taxa comprise clusters of ancient cryptic species. Within the species investigated in detail, there was marked population genetic differentiation and strong phylogeographic structuring at a regional scale. Both taxa differ, however, in the extent of sympatry: whereas rotifer species show a high degree of sympatry, bryozoan species tend to be parapatric or allopatric. We will discuss how the parallels and differences in life history, habitat feature and the presence of time-travel propagules help to explain these results, and explore the consequences of these for the diversification and evolution of cryptic species complexes.

26.5

THE USE OF DNA TAXONOMY FOR SPECIES INVENTORIES

[1]**D. Tautz**, [1]A. Pozhitkov, [2]M. Markmann

[1]*University of Cologne, Department of Genetics, 50931 Cologne, Germany*

[2]*GeneData GmbH, Lena-Christ-Str. 50, 82152 Martinsrid, Germany*

Identification of species with molecular probes is likely to revolutionize taxonomy, at least for taxa with morphological characters that are difficult to determine otherwise. Among these are the single cell eucaryotes, such as Ciliates and Flagellates, but also many other kinds of small organisms, such as Nematodes, Rotifers, Crustaceans, mites, Annelids or Insect larvae. These organisms constitute the meiofauna in water and soil, which is of profound importance in the ecological network. Efficient ways for monitoring species identity and abundance in the meiofauna should significantly help to understand ecological processes. We use the principles of DNA Taxonomy (Tautz et al. 2003) to develop fast assessment tools for complex mixtures of species. One approach is based on the selection of species-specific oligo-nucleotides that can be used in microarray experiments (Pozhitkov and Tautz 2002). Another approach aims at developing cheap and simple sequencing technologies. We believe that these tools will eventually allow to do species inventories and monitoring on a routine basis and at low costs per sample. Examples will be based on a data basis for benthos organisms of Bavarian lakes (Markmann 2000).

Cited references: Pozhitkov A, Tautz D (2002). An algorithm and program for finding sequence specific oligo-nucleotide probes for species identification. BMC Bioinformatics 3, 9. Tautz D, Arctander P, Minelli A, Thomas RH, Vogler AP (2003). A plea for DNA taxonomy. Trends in Ecology and Evolution 18, 70-74. Makmann M (2000). Entwicklung und Anwendung einer 28S rDNA-Sequenzdatenbank zur Aufschlüsselung der Artenvielfalt limnischer meiobenthosfauna in Hinblick auf den Einsatz moderner Chiptechnologie. Dissertation, University of Munich.

26.6

SPECIATION AS A POSITIVE FEEDBACK LOOP BETWEEN PRE- AND POSTZYGOTIC BARRIERS TO GENE FLOW

G.–P. Saetre, M. R. Servedio,

Dept. of Biology, Div. of Zoology, University of Oslo, P.O. Box 1050 Blindern, N-0316 Oslo, Norway

Speciation is intimately associated with the evolution of sex and reproduction related traits, including those affecting hybrid incompatibility (postzygotic isolation) and species recognition (prezygotic isolation). Genes controlling such traits are not randomly distributed in the genome but are particularly abundant on the sex chromosomes. Yet, the evolutionary consequences of sex linkage of genes involved in speciation have been little explored. Here we present simulations of a continent-island diploid model that examines the effects of reduced recombination using both autosomal and sex-linked inheritance. We show first that linkage between genes affecting post- and prezygotic isolation leads to a positive feedback loop in which both are strengthened. As species recognition evolves, genes causing hybrid incompatibility will hitchhike along with those improving premating isolation, leading to stronger hybrid incompatibility and thus increased pressure for further preference divergence. Second, we show that this loop effect is generally enhanced by sex linkage because recombination is eliminated in the heterogametic sex, leading to tighter effective linkage between the two classes of genes, and because natural selection is more efficient at sex-linked loci, since recessive alleles are not masked by dominance in the heterogametic sex. Accordingly, hitchhiking can be important in promoting speciation and can also lead to increased postzygotic isolation through adaptive evolution. We have tested some key assumptions and predictions of the loop hypothesis on the *Ficedula* flycatcher model system. The patterns observed are consistent with the hypothesis.

26.7

SPECIATION PROCESSES AND HOST PLANT UTILIZATION IN POLYGONIA BUTTERFLIES

Elisabet Weingartner, Soren Nylin, Niklas Wahlberg,

Department of Zoology, University of Stockholm, Svante Arrhenius vag 14, 106 91 Stockholm, Sweden

Polyphagy in Nymphalini (Nymphalidae, Lepidoptera) has been suggested to be a transient phase where species can shift to novel host plants or respecialize to ancient ones (Janz et al., 2001). Shifts to novel host plants might be a factor leading to speciation. The tribe Nymphalini and its host plant use has been studied theoretically and empirically by Nylin and his group at the University of Stockholm. I will report on a study of the speciation processes in the polyphagous genus *Polygonia* (Nymphalidae, Lepidoptera). I have worked on a phylogeny of the genus *Polygonia* and a more detailed phylogeographic study of selected species in *Polygonia* based on the mitochondrial gene COI. The study aims to get a better understanding of the processes of host plant use, geographic distribution and speciation and the relationships between those mechanisms in the tribe. With such an understanding we can try to answer the question of whether polyphagy has led to greater distribution range and speciation in this tribe.

26.8

MODELS OF SYMPATRIC SPECIATION: FACTS AND DELUSIONS

Sergey Gavrilets

Department of Ecology and Evolutionary Biology, Uiversity of Tennessee, Knoxville, TN 37919 USA

I will review several simple models of sympatric speciation which can be studied without having to rely on complicated numerical simulations. These models lead to more transparent conclusions about the plausibility of sympatric speciation in natural populations.

26.9

SPECIATION AND COSPECIATION IN QUANTITATIVE GENETIC MODELS

Barbara Drossel, Arijit Bhattarcharyay,

Institute of Solid State Physics, TU Darmstadt, Hochschulstr.6, D-64289 Darmstadt

We model sympatric speciation using quantitative genetic models and natural selection based on Lotka-Volterra type competition equations. Starting from earlier work by one of the authors (Drossel & McKane (2000), J. Theor. Biol. 204, 467-478; Drossel (2001), Adv. Phys. 50, 209-295), we show that this approach can be extended to the coevolution and speciation of flowers and pollinators, if the interaction between the two species is included in the model. We discuss under which conditions the model favors speciation and mutual specialisation over generalist behavior. We present several different possible scenarios. Among these are the speciation of the flowers in the presence of several pollinator species, and the cospeciation of both. Situations with and without the red queen effect are mentioned. The role of a geographic gradient and of other factors is discussed.

26.10

MODELING EVOLUTIONARY AND ECOLOGICAL CONSEQUENCES OF SELECTION IN HETEROGENEOUS ENVIRONMENTS

Dan Cohen

The Hebrew University, Evolution, Systematics, and Ecology Dept., Jerusalem 91904, Israel

1. Individuals in natural populations are exposed to a wide range of different selective conditions. 2. The force of selection that operates on individuals exposed to any one condition of type i is proportional to the fraction Fi of the reproductive output of the exposed population. 3. Selection on any one locus or trait A in a large mixed population establishes an allele or trait value A* which maximizes the mean fitness W^(A)= Sum(Wi(A)Fi), weighted over all the conditions according to their fitness functions and fractions of reproductive outputs: 4. The degree of adaptation of any trait to any one of the many rare specific conditions depends only to a small extent on each specific selection coefficient! 5. The condition-specific adaptation depends therefore almost only on the correlations between the fitness of the mean optimal A* allele or trait and the fitness of the specific optimal allele or trait Ai* at each specific condition. 6. Species are expected to be better adapted and to exploit mostly their more common and more positively correlated habitats or life conditions, which have positively correlated fitness functions. 7. Opening a large new habitat to a species may select against adaptation to some habitats with negatively correlated fitness functions. An elimination of a large habitat may select for an adaptive shift to previously unexploited rare habitats. 8. A superior competitive species is not very likely to evolve to displace and exclude coexisting rare species that exploit rare negatively correlated habitats. 9. The exploitation by one species of habitats or resources with negatively correlated fitness functions is ecologically and genetically unstable. Such habitats or resources may remain unexploited by existing species.

26.11

EVOLUTION OF MITOCHONDRIAL INHERITANCE IN MUSSELS FROM BALTIC SEA

Artur Burzynski, Tomasz Kijewski, Malgorzata Zbawicka, Roman Wenne,

ZGiBM IO Polish Academy of Sciences, Powstancow Warszawy 55, 81-712 Sopot, Poland

Mussels from the genus *Mytilus* are known to exhibit a very particular mode of mitochondrial DNA inheritance, so called Doubly Uniparental Inheritance (DUI). Contrary to the vast majority of other animals their mitochondrial inheritance is not strictly maternal. Males contribute to the offspring mtDNA pool by transferring their mitochondria to sons. That way two separate lines of mitochondrial inheritance exist with two highly divergent M and F genomes present in heteroplasmic males. Baltic population of *Mytilus* mussels was long considered to consist of dwarf *Mytilus edulis* being in fact an ecotype associated with lower salinity. The discovery of allozymatic markers diagnostic for *Mytilus trossulus* in the Baltic brought up the issue of taxonomic identity of this ecotype. Our studies show that Baltic population consists of hybrids having nuclear markers from both species but no mitochondrial markers of *M. trossulus*. Moreover, under this apparent cytonuclear disequilibrium, DUI is maintained but the original M genome is being replaced by new genomes emerging from F line. Those new M genomes acquire M-type regulatory region by recombination. The possibility that this type of control region conversion may have accompanied speciation and may in fact underline the evolution of DUI in Bivalves is discussed.

26.12

DIVERSIFICATION IN SEXUALS AND ASEXUALS

Timothy G. Barraclough

Imperial College London, Silwood Park Campus, Ascot, Berkshire, Sl5 7PY

Sexual reproduction has long been proposed as a major factor explaining the existence of species and species diversity. But the importance of sex for diversification remains obscure because of the lack of theoretical treatments, difficulties of applying universal concepts of species and speciation, and above all the scarcity of empirical tests. I use genealogical theory to compare the relative tendency of strictly sexual and asexual organisms to diversify into discrete genotypic and morphological clusters. Asexuals are expected to display discrete clusters similar to those found in sexual organisms. Whether asexuals or asexuals display stronger clustering depends on a number of factors, but in at least some scenarios asexuals should display a stronger pattern. Confounding factors aside, the only explanation for stronger patterns of diversification in sexuals than asexuals is if faster rates of adaptive change conferred by sexual reproduction promote greater clustering. Empirical comparisons of diversification in related sexual and asexual taxa are needed to resolve this issue.

26.13

MOLECULAR SYSTEMATICS OF EUTHYNEURA (MOLLUSCA: GASTROPODA)

[1]**C. Grande**, [1]J. Templado, [2]J. L. Cervera, [1]R. Zardoya

[1]*Museo Nacional Ciencias Naturales, CSIC. Madrid, Spain*

[2]*Universidad de Cádiz. Cádiz, Spain*

Euthyneura is a monophyletic group of gastropods including opisthobranchs and pulmonates. However, the monophyly of both Opisthobranchia and Pulmonata is under discussion based on morphological and molecular data. Previous studies have shown that phylogenetic inferences based on morphological approaches lack consistency due to extensive homoplasy. On the other hand, molecular studies have been based on rather short sequence data sets and limited taxon sampling. To test the monophyly of both opisthobranchs and pulmonates, nucleotide sequences of three mitochondrial genes (16S rRNA, tRNA-val and COI, about 2500 b.p.) have been sequenced for 40 families of Opisthobranchia and Pulmonata. We have also sequenced another mitochondrial fragment (including the complete sequences of the ND6, tRNA-lys, tRNA-ala, tRNA-pro genes and partial sequence of the ND5 gene, about 1200 b.p.) in several families to further understand euthyneuran systematics by investigating the evolution of tRNA gene arrangements onto the inferred phylogeny.

Posters

26.14P

PROKARYOTIC COMPLEXITY IS LIMITED BY REGULATORY OVERHEAD

[1]Larry J. Croft, [2]Martin J. Lercher, [1]Michael J. Gagen, [1]John S. Mattick

[1]*Institute for Molecular Bioscience, University of Queensland, Brisbane, Australia*

[2]*Dept. of Biology & Biochemistry, University of Bath, UK*

Increased biological complexity is generally associated with the addition of new genes, which in most cases will have to be integrated into the existing regulatory network that operates within the cell. Based on a simple model we argue that the number of regulatory factors should grow quadratically with increasing genome size. Analysis of 88 completely sequenced prokaryotic genomes demonstrates that this is indeed the case. Moreover, from comparison of the scaling of regulator number and operon number, we suggest that prokaryotic genomes with more than 10000 genes may be inefficient. This appears to be consistent with the observed ceiling on bacterial genome sizes. It suggests that prokaryotic complexity has been limited throughout evolution by regulatory overhead, rather than by environmental or biochemical factors, and conversely that complex eukaryotes must have bypassed this constraint by novel strategies, most likely through regulatory networks of noncoding RNAs.

26.15P

IMPLEMENTING MOLECULAR TECHNIQUES FOR NON-INVASIVE MONITORING OF IBERIAN CARNIVORES

[1]C. Ginja, [1]I. Pereira, [2]L. Zé-Zé, [2]R. Tenreiro, [3]M. W. Bruford, [1]M. Santos-Reis

[1]*Centro de Biologia Ambiental, Faculdade de Ciências de Lisboa, Portugal*

[2]*Centro de Genética e Biologia Molecular, Faculdade de Ciências de Lisboa, Portugal*

[3]*Cardiff School of Biosciences, Cardiff University, Wales – U.K.*

The use of non-invasive techniques in monitoring programmes for carnivores has been extremely valuable, since it allows the study of animals without the need to capture or even to observe them, and thus allows questions to be addressed that could not be answered with conventional methods. This project aims to have a major contribution in the development of a non-invasive strategy for monitoring Iberian carnivores using faeces as DNA source. The Portuguese community of Iberian carnivores is nowadays represented by 14 species, of which half are classified as threatened, comprising eight mustelids (*Mustela nivalis*, *Mustela erminea, Mustela putorius*, *Mustela vison*, *Martes foina, Martes Martes*, *Meles meles*, *Lutra lutra*), two felids (*Felis silvestris*, *Lynx pardinus*) one viverrid (*Genetta genetta)*, one herpestid (*Herpestes ichneumon*) and two canids (*Canis lupus*, *Vulpes vulpes*). Tissue, hair roots and faeces samples were collected from specimens resulting from capture programmes, road casualties or hunting activities. Total DNA was extracted using different extraction protocols, aiming optimisation and/or depending upon the sample type. In order to design species-specific primers that are likely to allow the analysis of short sequences amplified from degraded DNA (e.g. faeces), the entire *cytb* gene or overlapping segments of this gene of several individuals of each species were PCR amplified and sequenced using universal, mustelid-specific and internal primers. Some primers were also designed specifically for these analyses. Complete *cytb* sequences were obtained for several individuals of each species. Specific primers were designed for species assignment using scats. So far, molecular assays based on mtDNA sequences were performed to identify carnivore species from scats using these primers. In the future, the polymorphism of microsatellite loci will be studied as a method for detecting individual carnivores and sex determination using molecular scatology techniques.

26.16P

ECOLOGICAL AND GENETIC DIFFERECES ALONG A VERTICAL GRADIENT WITHIN A POPULATION OF INTERTIDAL GASTROPOD, *BATILLARIA CUMINGI* (BATILLARIIDAE)

O. Miura, M. Maki, S. Chiba

University of Tohoku, Aobayama, Sendai, Miyagi, Japan

Vertical zonation in the intertidal snail *Batillaria cumingi*, was studied in Ishinomaki Bay, Japan. The snails found in the highest part of the muddy shore possessed a larger shell with a longer spire than the snails from the lower tidal sites. Based on observations in the laboratory, the former prefers to stay above water to a greater extent than the latter, which corresponds to the difference in their intertidal heights. Among snails transplanted from the upper and lower tidal sites to the position boundary, most moved back to their original sites. Despite the differences in behavior and shell morphology between the snails from the upper and lower sites, no differences were observed in mitochondrial DNA sequences or anatomical characteristics except for the color of the hepatopancreas. Genetic variation was also compared between them. The variation at four highly polymorphic enzymes (PGI, LAP, SODH, G6PDH) were revealed in each type of *B. cumingi*. The results of genetic analyses show that genetic differentiation between the snails from upper and lower tidal sites was larger than that between the snails from the same shore level but horizontally aparted from each other. The above results suggest that the preferences for height and air-exposed/submerged condition on a tidal area are diversified within the populations of *B. cumingi*. This raises the possibility that the vertical zonation in the distribution of *Batillaria* species has arisen by the diversification of habitat preference within populations.

26.17P

NEW INSIGHTS INTO DEEP-NODE RELATIONSHIPS IN THE PHYLOGENY OF APHIDS (HOMOPTERA) USING THE LONG-WAVELENGTH OPSIN GENE

B. Ortiz-Rivas, J. M. Michelena, A. Moya, D. Martinez-Torres

University of Valencia, Apartado Correos 22085, 46071 Valencia, Spain

Viviparous aphids (Aphididae) constitute a monophyletic group within the order Homoptera comprising more than 4000 extant species mainly distributed in temperate regions. Their plant-sap-sucking way of feeding and their ability to transmit plant viruses to their hosts account for the status of crop pest of many of the species. Several other biological traits are of interest for evolutionary biologists. Among others, their complex and varied life cycles, with cyclical parthenogenesis associated in many groups with host alternation and elaborate polyphenisms, and the obligate symbiosis they maintain with intracellular bacteria (*Buchnera sp.*), have been the subject of intense research in recent years. Although knowing the phylogenetic relationships among major aphid taxa is relevant to these studies, no molecular approaches had been carried out until recently. Two recent reports attempted to clarify this issue with molecular data. However, both studies systematically found a lack of resolution of deep-node relationships, invoking a rapid adaptive radiation as a likely explanation. Here we present the results derived from the analysis of most of the long-wavelength opsin gene coding sequence of aphid representatives of seven subfamilies. These results corroborate some previously proposed relationships but contradict some others. They support the existence of three main clades, being the subfamily Lachninae one of them, which contradicts its generally accepted sistership relationship with the subfamily Aphidinae. Furthermore, our data also suggest a basal position of this subfamily, fact that has important implications on current discussions about the ancestrality of conifer-feeding in modern aphids. The relationships found in the other two clades (e.g. Aphidinae + Drepanosiphinae and Pemphiginae + Thelaxinae + Anoeciinae + Hormaphidinae) contradict those proposed in Heie's morphological aphid phylogeny, the most referenced hitherto, but roughly agree with Wojciechowski's alternative, as well as with some older proposals.

26.18P

POST-ZYGOTIC REPRODUCTIVE ISOLATION IN THE GUPPY, *POECILIA RETICULATA*

[1]Stephen T. Russell, [2]Anne E. Magurran

[1]*University of St. Andrews, Bute Medical Buildings, St. Andrews, Scotland.*

[2]*University of St. Andrews, Gatty Marine Laboratory, St. Andrews, Scotland*

Trinidadian populations of the guppy, *Poecilia reticulata*, are becoming an important model in exploring the evolution of reproductive isolation. Despite strong potential for genetic correlations between male traits and female preferences to induce sexual isolation between populations, such isolation remains generally weak. Nevertheless, post-zygotic reproductive isolation seems appreciable, at least between highly genetically divergent lineages. We established laboratory crosses between Lower Tacarigua River (Caroni Drainage) and Oropuche River (Oropuche Drainage) populations that have been separated for ~2 – 2.5 myr. Both reciprocal F1 crosses did not differ significantly from parental controls in fertility, survival rates, adult sex-ratio or sperm counts. In contrast, behavioural inviability of F1 males (reduced numbers of sneaky matings and courtship displays) was usually significant suggesting that extrinsic isolation evolves more rapidly than intrinsic isolation. Intrinsic isolation did, however, become evident in the F2 generation with F2 crosses showing greatly reduced fertility.

26.19P

HIGH GENETIC VARIABILITY WITHIN AND AMONG NATURAL POPULATIONS OF *ARABIDOPSIS THALIANA* FROM NORTHERN EUROPE

[1]Hans K. Stenoien, [2]A.Tonteri, [3]Charles B.Fenster, [2]O. Savolainen

[1]*Uppsala University, Evolutionary Biology Centre, Department of Plant Ecology, Villav. 14, SE-752 36 Uppsala, Sweden*

[2]*University of Oulu, Department of Biology, PO Box 3000, Fin-90014 Oulu, Finland*

[3]*University of Maryland, Department of Biology, College Park, Maryland 20742, USA*

Ten natural populations of *Arabidopsis thaliana* from Norway were subjected to studies of genetic diversity and structure at 25 microsatellite loci. The populations were situated along a North-South gradient ranging from 57' N to 69' N, the latter representing the northernmost margin of this species distribution in Europe. 84% (i.e. 21) of the loci were polymorphic, and six of the populations contained within-population variability. In the polymorphic populations, mean gene diversities over loci ranged from 0.02 to 0.22. There was no association between gene diversity and population size. The northernmost population had a seemingly small population size, but was relatively variable, with 3 multilocus genotypes, and a mean gene diversity of 0.11. This seems not consistent with the hypothesis of greater variability in the centre of species distribution compared to the periphery. One population from Southern Norway was particularly variable, also containing several heterozygotes. All populations were strongly differentiated based on Fst-estimates, and differentiation was not correlated with geographical distance. These patterns of putatively neutral genetic structuring suggest that differentiation in studied morphological characters have an adaptive significance in these populations.

26.20P

INTERSPECIFIC AGGRESSION, CHARACTER DISPLACEMENT AND SELECTION ON SEXUAL CHARACTERS IN THE DAMSELFLY

[1]Katja Tynkkynen, [1]Janne S Kotiaho, [1]Mari Luojumäki, [2]Markus J. Rantala, [1]Jukka Suhonen

[1]*Department of Biological and Environmental Science, P. O. Box 35 (YAC), FIN–40014 University of Jyväskylä, Finland*

[2]*Current address: Department of Biology, University of California, Riverside, CA 92521, USA*

Problems in species recognition are thought to affect the evolution of secondary sexual characters mainly through hybridization. Another, but much less studied, avenue for evolution of sexual characters due to species recognition problems is through interspecific aggression. In territorial damselfly *Calopteryx splendens* males have sexually selected pigmented wing spots, the size of which indicate male quality. Large spotted males resemble males of another species, *Calopteryx virgo*, causing potential problems in species recognition. Here we present a set of experiments designed to investigate whether there is character displacement in wing spot size and whether interspecific aggression could cause that pattern. Interestingly, wing spot size of *C. splendens* decreased with increasing relative abundance of *C. virgo* in the population. Two lines of evidence suggest that interspecific aggression from *C. virgo* males may explain this pattern of character displacement. First interspecific aggression was more intense towards large than small spotted *C. splendens* males, and second in interspecific contests *C. virgo* males were better able to defend their territories than *C. splendens* males. In addition, we found that directional survival selection on wing spot size was inversely related to relative abundance of *C. virgo* males, and that the trend was changed by experimental removal of *C. virgo* males. Thus, interspecific aggression may be an evolutionarily significant force that is able to cause divergence in secondary sexual characters.

26.21P

NUCLEOTIDE VARIATION AT SEVERAL NUCLEAR GENES IN *ANTIRRHINUM* WITH DIFFERENT MATING SYSTEMS

Tytti Vanhala, Deborah Charlesworth

University of Edinburgh/ICAPB, Ashworth Laboratories King's Buildings, Edinburgh EH9 3JT, Scotland UK

The mating system has a major influence on the pattern of genetic variation; an inbreeding population is expected to have less variation than an outcrossing population. We studied sequence variability of several single locus nuclear genes within and among four *Antirrhinum* species (*A. majus* ssp. *cirrhigerum*, *A. linkianum*, *A. meonanthum* and *A. molle*). Two populations of the studied *A. majus* ssp. *cirr.* were self incompatible and two were self compatible, while populations from the other *Antirrhinum* species were all self incompatible. Results from one gene, dehydroflavonol 4-reductase, show that the self incompatible populations have high variability. Within *A. majus* ssp. *cirr.* there is less silent site nucleotide variation in the self compatible than in the self incompatible populations. Several other genes are being sequenced to find out if they follow the same trend.

26.22P

ON THE EVOLUTIONARY HISTORY OF THE X/4 FUSION OF *DROSOPHILA AMERICANA*

Cristina P. Vieira, Jorge Vieira

IBMC, University of Porto, Rua do Campo Alegre 823, 4150-180, Porto, Portugal

In *Drosophila* there is limited evidence on the nature of evolutionary forces affecting chromosomal arrangements other than inversions. The study of the X/4 fusion polymorphism of *Drosophila americana* is thus of interest. Inferences on the chromosomal fusion history, on X-linked inversions, the size and structure of the *D. americana* population, recombination levels and selection are made based on five X-linked genes. So far the data suggests that crossing-over is suppressed at the base of the X chromosome between fusion and non-fusion chromosomes but not within fusion and non-fusion chromosomes. The data is compatible with previous claims, that within fusion chromosomes the amino acid clines found at fused1 (located at the base of the X chromosome) are likely maintained by local selection. The sequence data sets also suggest a young age of the X/4 fusion. There is no population structure other than that caused by the X/4 fusion itself. Therefore the data is compatible with previous claims that selection is maintaining the strong association observed between the methionine / threonine variants at fused1 and the status of the X chromosome as fused or unfused to the 4th chromosome.

Symposium 27

Limits to species' boundaries: linking hybrid zones with adaptation to marginal conditions

Organisers: Jon Bridle, Nick Barton, Tim Vines

Roger Stevens Lecture Theatre 22

09.50 – 10.20	**Kirkpatrick, M.** Evolution between Scylla and Charybdis: Gene flow and local adaptation
10.20 – 11.00	**Coffee**
11.00 – 11.30	**Lenormand, T.** The evolution of local adaptation
11.30 – 12.00	**Thomas, C. D.** The eco-evo dynamics of range boundaries
12.00 – 12.20	**Billard, S.** Evolution of migration in a spatially varying environment
12.20 – 12.40	**Bridle, J.** Individual based simulations of adaptation at range margins
12.20 – 14.00	**Lunch**
14.00 – 14.20	**Boulding, E. G.** Modelling the extinction risk of prey populations after an invasion of predators: Parameter estimates from an inter-tidal field experiment
14.20 – 14.40	**Pérez-Figueroa, A.** Evolutionary factors explaining polymorphism in *L. saxatilis*: computer simulations.
14.40 – 15.00	**Vines, T.** The role of habitat distribution in the structure of *Bombina* hybrid zones
15.00 – 15. 20	**Goodman, S.** Varying introgression among markers in a dynamic hybrid zone: Distinguishing selection from ancestral polymorphism and drift
15.20 – 16.00	**Tea**
16.00 – 16.20	**Polechova, J.** Speciation in asexual populations in sympatry and parapatry
16.20 – 16.40	**Nolte, A.** Hybrid zones of *Cottus* are fixed locally despite changes in population density
16.40 – 17. 00	**Jiggins, C. D.** Speciation in mimetic butterflies – range middle or margin?
17.00 – 17.20	**Barton, N.** Ecological and genetic limits to a species' range

Invited talks

27.1

EVOLUTION BETWEEN SCYLLA AND CHARYBDIS: GENE FLOW AND LOCAL ADAPTATION

Mark Kirkpatrick

School of Biological Sciences, University of Texas, Austin, TX78712

Gene flow plays contrasting roles in evolution: it can frustrate local adaptation, but can also alleviate inbreeding depression. In the first role, models show how and when gene flow can constrain the geographic range and ecological niche of a species that inhabits a world that varies in space due to abiotic factors or coevolving species. In the second role, inbreeding depression in residents can give rare immigrants a reproductive advantage. Results from a natural population of *Daphnia* can be used in conjunction with theory to show that this effect can greatly magnify the genetic consequences of gene flow, and in some cases can enhance introgression between species.

27.2

THE EVOLUTION OF LOCAL ADAPTATION

Thomas Lenormand

CEFE - UPR 9056 CNRS; 1919 route de Mende; F-34293 Montpellier Cedex 5

When there is a sudden environmental change in a region within a species range, different evolutionary outcomes are possible (1) the species range may decrease and exclude this region (2) speciation could occur with a new species occupying this region and (3) some new adaptive traits may spread and the species range remain unchanged. I will discuss, using theoretical models and empirical data on the evolution of insecticide resistance, the different factors influencing the outcome of this regression / speciation / adaptation scenario. I will draw a parallel between studies of hybrid zones and local adaptations and finally show how what we learn from the study of local adaptation can be incorporated and extend the five major elements of speciation synthesised by Kirkpatrick and Ravigné (2003).

27.3

THE ECO-EVO DYNAMICS OF RANGE BOUNDARIES

Chris Thomas

School of Biology, University of Leeds, LS2 9JT, UK

It is suggested that range boundaries typically existing in two alternative states: stable (or declining) and expanding. Population and evolutionary dynamics typically lead to relatively low dispersal, specialised populations at stable boundaries, in a feedback loop. At expanding boundaries, generalist and high dispersal traits are favoured, resulting in further gene flow among populations. The produce an alternative feedback loop at expanding fronts. Butterfly and bush cricket systems are described to illustrate these dynamics.

Contributed talks

27.4

EVOLUTION OF MIGRATION IN A SPATIALLY VARYING ENVIRONMENT

[1]**Sylvain Billiard,** [2]Thomas Lenormand

[1]*Universté Montpellier II, CC 065, Place Eugène Bataillon, 34000 Montpeliier, France*

[2]*CEFE, Route de Mende, 34000, Montpellier, France*

In Kirkpatrick and Barton's (1997) model of evolution of a species' range, the migration rate is supposed fixed. However, migration is indirectly selected against in a spatially varying environment because of local adaptation: Migrants can land in a habitat to which they are maladapted. Classical models of evolution of migration in a heterogeneous environment found that the optimal migration is zero. Under which conditions migration could be maintained Kirkpatrick and Barton's (1997) model? Migration may be favoured because it decreases kin competition. The intensity of kin competition may be different in the habitats because of random drift. With low migration and high drift, the difference of the kin competition intensity between habitats is high and migration is favoured. However, when migration increases, the difference of intensity decreases and then the benefit to migrate is smaller. Hence, as the cost due to local adaptation, the benefit of migration depends on the migration itself. The model presented in this article captures these two effects and show that two non-zero ESS can coexist for the migration rate and consequently that migration can be maintained in heterogeneous environment and then explain the evolution of a species' range.

27.5

INDIVIDUAL-BASED SIMULATIONS OF ADAPTATION AT RANGE MARGINS

[1]**Jon Bridle** [2]Masakado Kawata, [3]Roger Butlin

[1]*Institute of Zoology, ZSL, London NW1 4RY*

[2]*University of Tohoku, Sendai, Japan*

[3]*School of Biology, University of Leeds, Leeds LS2 9JT*

Analytical models of species' edges make a number of predictions of the conditions under which adaptation to marginal habitats will be possible at a species' edge. One general conclusion of these models is that adaptation is possible at a wide range of parameters, particularly when the effects of increased genetic variance at the edge are taken into account. We will outline an individual-based simulation model for population spread along a selective gradient, which allows the potentially limiting effect of stochastic processes to be estimated. Additional complications such as epistasis and ecological patchiness are also considered. These results will be discussed in the general context of marginal vs parapatric adaptation, and the need for empirical tests of these theoretical parameters will be stressed.

27.6

MODELLING THE EXTINCTION RISK OF PREY POPULATIONS AFTER AN INVASION OF PREDATORS: PARAMETER ESTIMATES FROM AN INTERTIDAL FIELD EXPERIMENT

Elizabeth G. Boulding

Dept. of Zoology, University of Guelph, Guelph, Ontario N1G 2W1 Canada

Human activities have greatly increased the rate of introduction of exotic predators. Native prey populations may be unable to adapt to an invading predator, thereby risking extinction, because of high migration from populations still free of the predator. Consequently, to predict the outcome of predator invasions, we need to model the spatial arrangement of invaded and uninvaded prey populations. The predictions from such complex models should be tested in tractable systems using manipulative field experiments. An experimental predator invasion was created in September 1993 near Bamfield, B.C. (48°49'N; 124°41'W) by building cement refuges for predatory shore crabs (*Hemigrapsus nudus*) on two shores where they were normally rare. Crabs inhabiting the refuges preyed heavily on gastropod prey tethered next to the refuges, which caused strong directional selection for increased shell thickness in the two *L. subrotundata* populations located near the refuges but no selection in five populations located more than three meters away. Migration rates among contiguous populations were high even though *L. subrotundata* lacks a free-swimming larval stage. Data from the field experiment were used to parameterize a new spatially explicit, individual-based, finite locus model where the predator resistance of the gastropod prey populations was modelled as a single quantitative trait. Important parameters influencing the probability of extinction were the number of adjacent populations in the "core area" invaded by the predator and the amount of gene flow from surrounding predator-free populations. The parameterized model predicts slow and very limited adaptation to the presence of the shore crabs, which matches our experimental results so far, and rapid and complete adaptation if a greater proportion of the populations were near a crab refuge. Our conclusion is that very localized biotic changes may be more likely to cause extinction than more widespread changes that affect neighbouring populations as well.

27.7

EVOLUTIONARY FACTORS EXPLAINING A POLYMORPHISM IN *LITTORINA SAXATILIS*: COMPUTER SIMULATIONS

A. Pérez-Figueroa, R. Cruz, F. Carvajal-Rodríguez, E. Rolán-Alvarez, A. Caballero

Departamento de Bioquímica, Genética e Inmunología. Facultad de Ciencias. Universidad de Vigo. 36200 Vigo Spain

Two rocky shore ecotypes of *Littorina saxatilis* (RB and SU) from NW Spain live at different shore levels and habitats, albeit they still maintain some gene flow hybridising at the mid shore. These ecotypes differ at many behavioural, morphological and life history traits, and have already developed an incomplete reproductive isolation through size assortative mating. Thus, this polymorphism has been claimed as an example of sympatric ecological speciation. Several experiments have indicated that different evolutionary factors (migration, assortative mating and habitat-dependent selection) have a role on the maintenance of the polymorphism, but theoretical support on this hypothesis is absent. We have developed a computer simulation model to assess the role of different evolutionary mechanisms on the maintenance of the polymorphism. A matrix deterministic model was also used to validate the simulation approach in simple situations. We evaluate the concordance between the simulation output and some experimental estimates obtained from the wild (concordance index) under an orthogonal combination of four evolutionary factors (gene flow, reproductive isolation, selection in pure zones and selection in the mid-shore). The role of the number of genes selected and their effects, different amounts of environmental variation, the definition of the hybrid ecotype and the effects of phenotypic plasticity were also investigated. The results show that the fittest model (with the highest concordance values) presented high gene flow ($Nm > 8$), intermediate reproductive isolation between ecotypes (isolation index $Ic = 0,67$) and strong selection against the allopatric ecotypes on each shore level (non-resident ecotypes fitness < 1). Interactions were typically significant but with smaller effects than main factors. The ecotype fitness at the mid-shore, the number of genes involved, the level of phenotypic plasticity or the environmental effects were not fundamental factors to explain the present polymorphism.

27.8

THE ROLE OF HABITAT DISTRIBUTION IN THE STRUCTURE OF *BOMBINA* HYBRID ZONES

[1]**T. H. Vines**, [2]B. Nurnberger, [1]N. H. Barton

[1]*ICAPB, University of Edinburgh, Edinburgh EH9 3JT, Scotland*

[2]*Department Biologie II, Ludwig Maximillian University, D- 80333 Munich, Germany*

Mosaic hybrid zones arise when ecologically differentiated taxa hybridize across a network of habitat patches. Frequent interbreeding across a small scale patchwork can erode species differences that might have been preserved in a clinal hybrid zone. We present here a case study of a mosaic hybrid zone between the fire-bellied toads *Bombina bombina* and *B. variegata* in Romania. In our 20 x 20 km study area, we detected no evidence of a clinal transition but found a strong association between aquatic habitat and mean allele frequencies at four molecular markers. In particular, pure populations *of B. bombina* in ponds appear to cause massive introgression into the surrounding *B. variegata* gene pool found in temporary aquatic sites. While plausible selection strengths can maintain differentiation at those loci adapting the toads to either permanent or temporary breeding sites, the divergence at neutral markers must be transient. The hybrid zone may be approaching a state in which the gene pools are homogenized at all but the selected loci, not dissimilar from an early stage of sympatric divergence.

27.9

VARYING INTROGRESSION AMONG MARKERS IN A DYNAMIC HYBRID ZONE: DISTINGUISHING SELECTION FROM ANCESTRAL POLYMORPHISM AND DRIFT

[1]**Simon Goodman**, [2]Nick Barton, [2]Grahame Swanson, [2]Josephine Pemberton

[1]*Institute of Zoology, ZSL, London NW1 4RY*

[2]*ICAPB, University of Edinburgh, EH9 3JT*

Studying differential rates of introgression among markers and traits in hybridising taxa provides an insight into the mechanisms that determine the spread of genotypes into novel genetic backgrounds. However, in empirical studies, distinguishing variation in introgression driven by selection from stochastic variation due to drift or from ancestral polymorphism can be problematic. When hybridisation occurs through a low rate of F1 generation followed by backcrossing into the parental populations, random assortment and segregation alone can generate significant variation in introgression among loci. This may mimic the pattern expected where loci experience differing levels of positive or negative selection driving or impeding introgression into the opposite parental population. Loci can also vary in the frequency of shared ancestral polymorphisms that can be confused with introgressed alleles derived from recent hybridisation events. In a recently initiated and moving hybridisation event among native red deer (*Cervus elaphus*) and introduced Japanese sika deer (*Cervus nippon*) in Argyll, Scotland, significant variation in introgression exists among 25 'species diagnostic' microsatellite loci for a survey of 247 sika-like deer and 416 red-like deer. In both taxa about 30% loci exhibited significantly less introgression than expected, while 12% and 4% of loci showed significantly greater introgression in sika-like and red-like deer respectively. This variation introgression was primarily seen in backcrossed 'ancient' hybrids, rather than animals of recent hybrid origin with multiple introgressed alleles. However, simulations suggest the observed variation cannot be distinguished from the pattern expected from drift under the conditions of rare hybridisation and backcrossing, and the genotypic composition of recent hybrids suggest few F1s contributed to the current pool of introgressed in the populations. Here we show how the spatial distribution of genotypes in the hybrid zone can be used to resolve if selection is driving the observed variation introgression.

27.10

SPECIATION IN ASEXUAL POPULATIONS IN SYMPATRY & PARAPATRY

[1]**Jitka Polechova**, [2]Nick Barton

[1]*Charles University in Prague, Vinicna 7, Praha 2, 128 45, Czech Republic*

[2]*ICAPB, University of Edinburgh, Edinburgh EH9 3JT, Scotland*

While biogeographic evidence and theory have led to the view that allopatric divergence predominates, recent theory has relaxed the constraints on sympatric and parapatric speciation. Dieckmann and Doebeli (1999) claim a rather high probability of sympatric speciation in single populations with unimodal carrying capacity, for both asexually and sexually reproducing populations. In a subsequent model (2003) these authors argue that clumping due to frequency-dependent competition is even more likely in spatially structured populations along an environmental gradient. We concentrate on the asexual model and assess possible causes of clumping to discrete phenotypes. Specifically, we argue that in sympatric populations with frequency-dependent competition as modelled in DD (1999) two discrete phenotypes can be stable for a reasonably long time only under rather limited conditions. Conversely, the unimodal equilibrium predicted by Roughgarden (1972) will be filled by more phenotypes, so that there is negligible disruptive selection necessary for reinforcement. Here, we show that in DD's (2003) model, parapatric clumping emerges naturally when the spatial range is limited, as a result of reduced maladaptive gene flow at the edges. We also analyse the importance of this phenomenon for phenotypic clumping in asexual populations, and assess the importance of random drift and other irregularities in the system.

27.11

HYBRID ZONES OF *COTTUS* ARE FIXED LOCALLY DESPITE CHANGES OF POPULATION DENSITY OF DIVERGENT POPULATIONS

[1]**A. Nolte**, [1]D. Tautz, [2]J. Freyhof

[1]*University of Cologne, Institute for Genetics, Weyertal 121, 50931 Cologne, Germany*

[2]*Institute for Freshwater Ecology and Inland Fisheries, Dept. 4, 12587 Berlin, Germany*

We have identified divergent types of *Cottus gobio* L.1758, which occur in a parapatric pattern within the lower Rhine drainage. Besides morphological and genetic differentiation the two types strongly diverge in their autecological potential to colonize ecological subregions within a continuous river system. While the stream type is confined to the rhitral (cold headwaters) the river type lives in the potamal (summerwarm lower reaches of bigger rivers). Within these subregions they realise divergent life history strategies. Genetic analysis revealed that the divergent types form multiple extremely narrow hybrid zones in areas where small streams enter larger rivers. Here we show, how field data on population dynamics on both sides of narrow hybrid zones allow simple inferences about the type of selection that is prevalent. Data from a ten - year monitoring program demonstrate highly asymmetric population dynamics of the parapatric types. Population densities seem to be of low importance for the positioning of the hybrid zones. The general pattern observed can be explained by differential adaptation to stream and river environments and external selection pressures.

27.12

SPECIATION IN MIMETIC BUTTERFLIES: RANGE MIDDLE OR RANGE MARGIN?

Chris D. Jiggins

ICAPB, University of Edinburgh

Many *Heliconius* species are divided into distinct colour pattern races. Here I present evidence that mate preferences have co-evolved with colour pattern, such that males preferentially court females with their own wing pattern. Nonetheless, where such races meet, colour pattern genes are in Hardy-Weinberg equilibrium, suggesting random mating. Therefore, mate preferences break down in hybrid zones and pre-mating isolation probably arises through co-evolution of mate choice with colour pattern in widespread populations, rather than reinforcement in hybrid zones. Epistasis of preference and pattern genes means that pre-mating isolation builds up even between races separated by hybrid zones. In conclusion, initial divergence in pattern may occur in marginal populations where genetic drift and distinct mimetic faunas are more likely, but pre-mating isolation subsequently arises in the centre of the range, away from hybrid zones or margins. Mate choice tests from across the species range are needed to further test these hypotheses.

27.13

ECOLOGICAL AND GENETIC LIMITS TO A SPECIES' RANGE

Nick Barton

ICAPB, University of Edinburgh, Edinburgh EH9 3JT, Scotland

A species' range may be limited by failure to adapt to changing conditions, or by hybridisation with close relatives. Moreover, species may form as these boundaries evolve within a parapatric distribution. Although these different kinds of species' boundary have been discussed in different contexts, it is helpful to see them within one framework. I discuss the relation between ecological models of range limits, parapatric speciation, and hybrid zones. In particular, I show that surprisingly low rates of introgression can cause local populations to collapse, so that strong reproductive isolation may be necessary for expansion into novel environments.

Posters

27.14P

MECHANISMS MAINTAINING THE CROW *CORVUS CORONE* HYBRID ZONE AND ITS STABILITY

F. Haas, A. Brodin

Lund University, Dep. of Theoretical Ecology, Ecology Building, 223 62 Lund, Sweden

We have investigated the Crow hybrid zone in southern Denmark and northern Germany. By comparing the present distribution of the hybrid zone with detailed data from the beginning of the last century we can conclude that the zone has remained more or less stable over the past 80 years. One mechanism that can contribute to the maintenance of hybrid zones is assortative mating. In this study we have documented assortative mating, but the results are contradictory. Judged from phenotypic characters somewhat less than 30 percent of the individuals in breeding pairs are hybrids in the central part of the hybrid zone. A comparison between observed and expected numbers of different pair constellations (hooded – hooded, hooded – carrion, hooded – hybrid and so on) shows that the Hooded *C. c. cornix* and Carrion Crows *C. c. corone* tend to avoid each other when it comes to partner choice. But pairs where at least one of the individuals is of hybrid phenotype are found in numbers that would be expected by chance. Thus, there seems to be no disadvantage for hybrids from mate choice. On the other hand "pure" phenotypes produce less hybrid offspring than expected. Local environmental conditions may determine the local equilibrium position of the zone without necessarily affecting other characteristics. A preliminary analysis of land cover data indicates that the occurrence of pastures coincides with the distribution of Carrion Crows. South of the line where equal numbers of Hooded and Carrion Crows are found the land is very much influenced by pastures, which is not the case north of the 50:50 line.

27.15P

THE OXFORD-HERMITAGE COMMON SHREW HYBRID ZONE - A GIS APPROACH

R. M. Jones, J. B. Searle

Department of Biology, University of York, PO Box 373, York YO10 5YW, UK

Within Britain there are three karyotypic races of the common shrew (*Sorex araneus*). These races occupy relatively exclusive areas, forming hybrid zones on contact. The position of the hybrid zone between the Oxford and Hermitage races can be mapped according to the position of their race specific chromosome clines, which are staggered from each other. A method of plotting the course of the zone in a Geographic Information System (GIS) is described, allowing it to be related to environmental features, such as altitude, which may be important in determining its position.

27.16P

ADAPTIVE VARIATION IN GROWTH EFFICIENCIES AMONG POPULATIONS OF THE COMMON FROG, *RANA TEMPORARIA*, AT DIFFERENT LATITUDES

Beatrice Lindgren, Anssi Laurila

Uppsala University, Dept. of Population Biology/EBC, Norbyvägen 18D, 75236 Uppsala, Sweden

For ectotherms living in seasonal environments, time available for development and growth is often constrained by the length of the growth season. Declining season length towards higher latitudes may select for latitudinal clines in development and growth rates. However, the physiological mechanisms enabling these clines are not well understood. A simple explanation for differences in growth and development rates among populations is that they differ in food intake rate. Therefore, an obvious starting point for the determination of physiological mechanisms of growth rate variation is quantification of intake rates and growth efficiencies. In a laboratory experiment we raised tadpoles from eight common frog populations collected along a 1500 km latitudinal gradient across Sweden. The tadpoles were fed *ad libitum* and kept individually in two different temperature treatments for a total of 17 days. Weight increase, food consumption and gross growth efficiency (GGE) were measured in 20 tadpoles from each population. We found that populations from higher latitudes: increase in weight more rapidly, assimilate ingested food to increase body weight more efficiently and are not as constrained by lower temperatures as populations from more southern latitudes.

27.17P

CRYPTIC OR PSEUDO-CRYPTIC SPECIES IN THE PLANKTON

Alberto G. Saez, Colomban de Vargas

Imperial College London, Silwood Park, SL5 7PY, UK

Few studies have addressed species limits within the plankton. Recent studies on foraminifera indicate that most of the recognized species are in fact compounds of several "cryptic" or "pseudo-cryptic" species, long-ago evolutionarily splitted, yet morphologically barely indistinguishable. Our results on coccolithophores, a major planktonic group, and as the foraminifers key biostratigraphic marker fossils, suggest a parallel situation between both groups of planktonic organisms. We have isolated and cultivated numerous strains from five recognized species of coccolithophores, and then sequenced two to three different genes from them. As in foraminifers, we have found from two to three pseudo-cryptic species, with very clear limits that we have dated, for each of the described coccolithophorid species. These results are important in assesing marine biodiversity, interpreting the fossil record, and in helping us to "to think" - at least - about the speciation process in the planktonic realm. Relevant to this last point is that the revealed cryptic species from both, foraminifers and coccolithophores, present very often different ecological preferences, sometimes in sympatry but more often in different geographical areas.

27.18P

SPREADING INTROGRESSION IN THE WAKE OF A MOVING HYBRID ZONE

[1]Jean Secondi, [2]Bruno Faivre, [1]Staffan Bensch

[1]Department of Animal Ecology, Lund University, Sweden

[2]UMR CNRS 5561, Université de Bourgogne, Dijon, France

In spite of theoretical predictions to the contrary, hybrid zones have generally been considered as geographically stable units. However, an increasing number of studies, using long-term datasets or investigating biological invasions, have documented geographical zone shifts, thus raising the issue of how common this phenomenon is. Now, a major challenge is to design methods to detect zone movements when no historical records are available. Asymmetric clines with a longer introgression trail in the range of the expanding species are considered as good evidence of a shift. However, different marker types might not be equally informative in detecting introgression. In particular, recent evidence of selection on mtDNA makes its use as a marker controversial. We analysed mitochondrial and genomic variation in a well-documented moving avian contact zone in western Europe. We found no cross-species transfer of mtDNA and, using 30 AFLP markers, observed only one unambiguous hybrid. We did, however, detect an introgression trail in the expanding species. Surprisingly, introgression levels were higher in allopatric populations close to the zone than in the zone itself. This suggests that heterospecific genetic material spreads through either local recruitment or positive selection. In the latter case, integrating alien genes could benefit populations on the edge of the distribution range and contribute to its ongoing expansion. As expected, this moving hybrid zone is characterized by asymmetric introgression. However, mtDNA was not informative in detecting hybridization events, which suggests that mitochondrial data should be interpreted with caution.

27.19P

SPECIATION PATTERNS, HYBRID ZONES FORMATION AND THE EVOLUTION OF NEUTRALLY EVOLVING SEQUENCES IN INDIVIDUAL-BASED MODELS

[1]S. V. Semovski, [1]Yu. S. Bukin, [2]E. Verheyen, [1,3]D. Y. Sherbakov

[1]Limnological Institute SB RAS, Irkutsk, Russia

[2]Royal Belgian Institute of Natural Sciences, Brussels, Belgium

[3]The Irkutsk State University, Russia

We simulated the molecular evolution of a neutral nucleotide sequence using an individual-based model of population dynamics with mutation that involves disruptive selection. We show that the developed approach allows us to infer important details of evolutionary processes from a sub-sample of the sequences resulting a simulation. Evolution of population distributed in one-dimensional manifold is studied and this is considered as a model of benthic community on the littoral of ancient lake. Various patterns of allopatric, parapatric and sympatric speciation are arise depending on population viscosity, mobility of species and competition intensity. Dynamics of hybrid zones is investigated using distribution of resulting pairwise genetic distances between subpopulation. Simultaneous simulation of population evolution dynamics and neutral molecular evolution permits one to estimate the confidence limits for the observed rate at which new sequences evolve by analysing the shape of frequency distribution curve of the pairwise genetic distances among all the sequences. It is shown that this approach allows to distinguish between different scenarios of environmental changes which are important for speciation or intraspecific genetic diversification.

27.20P

POPULATION DIFFERENTIATION IN *SCHEDORHINOTERMES LAMANIANUS* IN EAST AFRICA - A BIOGEOGRAPHIC ANALYSIS

[1]L. Wilfert, [2]R. Brandl, [3]W. Durka, [4]M. Kaib

[1]*ETH Zurich, Ecology & Evolution, ETH Zentrum NW, 8092 Zurich, Switzerland*

[2]*Philipps-Universität, Karl-v.-Frisch-Str., 30532 Marburg, Germany*

[3]*UFZ Leipzig Halle, Theodor-Lieser-Str. 3, D-06120 Halle Saale, Germany*

[4]*Universiät Bayreuth, LS Tierphysiologie, D-95440 Bayreuth, Germany*

The humid forests adjacent to the east African coast have been divided from the Guineo-Congolian forest block in west and central Africa by an arid corridor since the early Pliocene. Possible past connections between these blocks as well as between the fragmented forests of east Africa are a central topic of African biogeography. The distribution of the African dampwood termite *Schedorhinotermes lamanianus* is closely associated with the humid forests of tropical and subtropical Africa. Its population structure was analysed in the present study from a biogeographic viewpoint in order to add to the understanding of these biotic relationships. Substantial population differentiation was demonstrated via both AFLP analysis and morphometric measurements, though the microgeographic population structures resolved within Kenya by these two marker systems were only partly congruent. The detected large-scale population structure is in accordance with the general biogeography of African forest biota. The separation of populations across the Great Rift Valley consistently shown by all employed marker systems demonstrates that this geographic feature does indeed represent a distributional barrier for this species. On a microgeographic level, the population structure of this study's focus taxon could not unequivocally be brought into accordance with a distributional model. Yet the results point to the island populations in the arid interior of Kenya being remnants of a wider distribution of *S. lamanianus* along an extensive network of gallery forests present during humid intervals in the Holocene.

Symposium 28

Evolutionary consequences of mate choice

Organisers: Martine Maan & Vicky Schneider

Roger Stevens Lecture Theatre 21

09.50 – 10.20	**Howard, R. S.** Mate choice and the evolutionary stability of sex
10.20 – 11.00	**Coffee**
11.00 – 11.30	**Siller, S.** Is there a lek paradox?
11.30 – 12.00	**Van Dooren, T. J. M.** Mate choice evolution and the odds of sympatric speciation vs. dimorphic sexes
12.00 – 12.20	**Van Doorn, G. S.** Sympatric speciation by sexual selection
12.20 – 12.40	**Klinkhamer, P. G. L.** Selective embryo abortion in plants
12.40 – 14.00	**Lunch**
14.00 – 14.20	**Barson, N. J.** Genetics of female mate preferences and speciation in Lake Malawi Cichlid fishes.
14.20 – 14.40	**Radwan, J.** Effectiveness of sexual selection in preventing fitness deterioration in bulb mite populations under relaxed natural selection
14.40 – 15.00	**Haavie, J.** Asymmetric character shifts in the song of sympatric pied and collared flycatchers (*Ficedula spp.*): a case of reinforcement?
15.00 – 15. 20	**Vistulo de Abreu, F.** Sympatric speciation from mutual sexual selection
15.20 – 16.00	**Tea**
16.00 – 16.20	**Bilde, T.** Implications of mate choice for inbreeding and the evolution of sociality in spiders
16.20 – 16.40	**Butcher, R. D. J.** Kin recognition based female mate discrimination in polyandrous wasps with an inbreeding sensitive sex determination system
16.40 – 17. 00	**Kurtz, J.** Mate choice for optimal immunity
17.00 – 17.20	**Alatalo, R. V.** Multitude of non-arbitrary male sexual ornaments in the lekking black grouse

Invited talks

28.1

MATE CHOICE AND THE EVOLUTIONARY STABILITY OF SEX

R. Stephen Howard

MTSU Dept. of Biology, Jones Hall 232, MTSU Box X087, Mufreesboro, TN 37132, USA

If sex functions to combat parasites, then sexual selection for disease resistance might increase the overall advantage to outcrossing. We used computer simulation to investigate how two forms of mate choice affect the stability of sex in populations of simultaneous hermaphrodites. In the first case, individuals preferred to mate with parasite-free individuals (condition-dependent choice). In the second form, individuals preferred mates having the least number of alleles in common at disease-resistance loci. We found that alleles encoding both forms of mate choice spread when rare, but their effects on the long-term stability of sex were different. Surprisingly, condition-dependent choice for parasite-free mates had minimal effect on the stability of sex. In contrast, choice for mates having different alleles at disease- resistance loci had a positive effect, especially under low rates to deleterious mutation. We suggest that mate choice that increases the genetic diversity of offspring can spread when rare in a randomly mating population, and, as an indirect consequence, increase the range of conditions under which sexual reproduction is evolutionarily stable.

28.2

IS THERE A LEK PARADOX?

Steven Siller

Department of Zoology, Oxford University, South Parks Road, Oxford OX1 1DP, United Kingdom

As has been economically expressed by Randerson et al. (2000):"Standard population genetics theory would predict that intense directional selection imposed by female choice will lead to a rapid loss of additive genetic variance for the male trait in question [and hence at loci reflected in the trait]. Should this occur, the benefits of female choice disappear." This is the so called "lek paradox" of Borgia (1979).

The verbal statement of the paradox presented above seems to be incontestable, and many theories have been proposed explain why females should show discrimination when mating with males who seemingly only provide genetic material.

The purpose of this talk is not to reject or provide an alternative to any of these proposed solutions, but to show that the "lek paradox" is based on a confusion between genetic variance and genetic variance in fitness. It neglects the fact that increasing female preference for a trait increases the marginal cost of an allele deleterious to that trait. It will be demonstrated that population genetics theory indeed predicts that modest discrimination by females may reduce the average number of deleterious mutations borne by individuals by two thirds or more. However, it is also shown that the conclusion that the benefits of female choice ineluctably diminish is not warranted. Increasing the intensity of selection on a set of loci, whilst decreasing the variance in the number of deleterious mutations, increases the contribution of these loci to genetic variance in fitness. It will be shown that the loss in variance of the trait, and hence the reduction in the heritable variation in viability and the reduction in the accuracy of phenotype mediated female discrimination, is more than balanced by the increased value to females of mating with the best male in the eyes of other females.

28.3

MATE CHOICE EVOLUTION AND THE ODDS OF SYMPATRIC SPECIATION VS. DIMORPHIC SEXES

Tom J. M. Van Dooren

Leiden University, Institute of Biology, Kaiserstraat 63, 2311GP Leiden, The Netherlands

Character displacement theory can explain the occurrence and evolution of ecologically dimorphic sexes and sympatric species. In complete sympatry, the odds between these two evolutionary solutions appear to be very uneven. Models show that sympatric speciation is very unlikely to happen if sexual dimorphism can evolve.

In principle, genetic constraints could tilt this balance, but they must be extremely strong in order to do so. Mate choice is more likely to make sympatric species evolve. If females already mate assortatively for their own ecological traits before character displacement can evolve, then sexes will never become different, only species will.

I investigate other possible effects of mate choice evolution on the odds of dimorphic sexes vs. sympatric species. To this end, different types of mate choice mechanism are added to a general resource competition model that can produce character displacement. Both mating and ecological traits are allowed to evolve. The main point of investigation is whether points in trait space where speciation can occur are easier or more difficult to reach when mate choice evolution is taken into account.

Contributed talks

28.4

SYMPATRIC SPECIATION BY SEXUAL SELECTION

[1]**G. Sander Van Doorn**, [2]Ulf Dieckmann, [1]Franz J.Weissing

[1]*University of Groningen/Centre for Ecological and Evolutionary Studies,Kerklaan 30, 9751 NN Haren, the Netherlands*

[2]*International Institute for Applied Systems Analysis/Adaptive Dynamics Network, Schlossplatz 1, A-2361 Laxenburg, Austria*

Recent verbal and formal models suggest that sympatric speciation may proceed by means of multiple divergent Fisherian runaway processes driven by sexual selection within a single population. This purported speciation mechanism agrees with observations and empirical results suggesting sexual selection as an important driving force of sympatric speciation. Notwithstanding this, here we show that classical Fisherian runaway models of sympatric speciation share three theoretical weaknesses: first, sexual selection may cause speciation only when populations start out from specific initial conditions, second, populations tend to evolve away from regimes of disruptive selection, and third, the stable co-existence of daughter species after speciation is not supported. We argue that these problems are general and are caused by the fact that classical models of female choice assume selection on female preferences to be frequency-independent. On this basis we present solutions to overcome the problem and demonstrate that sympatric speciation can still ensue from adaptive processes, driven by sexual selection, without introducing a dependence on external events or high mutation rates. This type of adaptive sympatric speciation, however, requires the action of mechanisms other than mate choice and only occurs under conditions far more restrictive than earlier, less detailed models of sympatric speciation by sexual selection would appear to suggest.

28.5

SELECTIVE EMBRYO ABORTION IN PLANTS

Peter G. L. Klinkhamer, Chantal Melser

University of Leiden, PO Box 9516, 2300 RA Leiden

Although plants cannot control which fathers deposit their pollen on the stigmas, there is potentially still ample opportunity for mate choice in plants. The maternal plant may affect pollen germination, pollen-tube growth, fertilization and seed and fruit abortion. For wild radish which has linearly arranged ovules (Marshall and Ellstrand 1988) assumed that pollen donors competing for ovule number and quality sort themselves out during fertilization. The maternal plants then set up a resource gradient from the basal to the stylar end of the fruit leading to position-dependent abortion. The combination leading to effective mate-choice. There is evidence for a number of species that plants can abort embryos selectively and that this selection leads to higher offspring quality. Such selection is not necessarily among potential fathers but may also be effective among the embryos sired by a single father. By aborting embryos with low potential fitness later in life, plants can free resources for the maturation of higher quality offspring. We studied the evolutionary consequences of selective seed abortion for the optimal division of resources over seeds (or fruits) and flowers. Based on experimental data on selective embryo abortion and the shape of the gain curve our model predicts that in *Echium vulgare*, which has four ovules per flower, selective seed abortion lowers the optimal seed to flower ratio in male steriles from a maximum of 4 to 1.8. In hermaphrodite individuals the effects of selective embryo abortion and sex allocation on the ES seed to flower ratio are intermingled. Together they reduce the ES-seed to flower ratio to 0.6. Similar results were obtained for the related *Cynoglossum officinale*.

28.6

GENETICS OF FEMALE MATE PREFERENCE AND SPECIATION IN LAKE MALAWI CICHLID FISHES

[1]**N. J. Barson**, [2]M. E. Knight, [1]G. F.Turner,

[1]*University of Hull, Cottingham Road, Hull, United Kingdom. HU6 7RX*

[2]*University of Southampton, Bassett Cresent East, Southampton, United Kingdom. SO16 7PX*

The cichlid fish species flocks of the East African Great Lakes are a classic example of explosive speciation. There are between 500 and 1000 endemic species of haplochromine cichlid within Lake Malawi all of which have radiated within the lake in the last 700,000 years. Although the subject of much debate, there is still no clear resolution as to why this group has speciated so much and so rapidly. Current evidence suggests that sexual selection could drive speciation in sympatry. Models show that the importance of sexual selection in speciation may be heavily dependent on the number of genes involved in pre-mating isolation. However to date this has not been empirically investigated. Experiments were conducted which examined whether female mate preference could be determined by a simple single locus mechanism in Lake Malawi cichlids, as has been assumed in some models. Mate choice of hybrid females from crosses between two closely related sympatric species was tested and compared to those expected from applying Mendelian genetic principles. The results have implications for the likelihood that sexual selection could be the driving force behind the explosive speciation of cichlids in the East African Great Lakes.

28.7

EFFECTIVENESS OF SEXUAL SELECTION IN PREVENTING FITNESS DETERIORATION IN BULB MITE POPULATIONS UNDER RELAXED NATURAL SELECTION

J. Radwan, J. Unrug, K. Znigórska, K. GawroDska,

Institute of Environmetnal Sciences, Jagiellonian University, ul. Ingardena 6, 30-060 Cracow, Poland

Under the good genes mechanism of sexual selection, females benefit from mate choice indirectly: their offspring inherit genes of the preferred, high quality fathers. Recent models assume that the genetic variance for male quality is maintained by deleterious mutations. Consequently, sexual selection can be predicted to remove deleterious mutations from populations. We tested this prediction by relaxing selection in populations of the bulb mite, thus increasing their rate of accumulation of deleterious mutation. Sexual selection, allowed to operate in half of these populations, did not prevent the fitness decline observed in the other half of the relaxed selection lines. After 11 generations of relaxed selection, female fecundity in lines in which males were allowed to compete for females declined compared to control populations by similar amount as in monogamous lines (17.5% and 14.5, respectively), while other fitness components (viability, longevity, male reproductive success) did not differ significantly between both types of lines and control populations.

28.8

ASYMMETRIC CHARACTER SHIFTS IN THE SONG OF SYMPATRIC PIED AND COLLARED FLYCATCHERS (*FICEDULA SPP.*): A CASE OF REINFORCEMENT?

[1]**Jon Haavie**, [1]Thomas Borge, [2]Stanislav Bures, [3]László Z. Garamszegi, [4]Helene M. Lampe, [5]Juan Moreno, [6]János Török, [7]Glenn-Peter Sætre

[1]*Department of Evolutionary Biology, Evolutionary Biology Centre, Uppsala University, Nordbyvägen 18D, SE-752 36 Uppsala, Sweden*

[2]*Palacky University, Laboratory of Ornithology, Tr. Svobody 26, 771 46 Olomouc, Czech Republic*

[3]*Department of Biology, Universitaire Instelling Antwerpen, UIA Universiteitsplein 1, B-2610 Wilrijk, Belgium*

[4]*Department of Biology, University of Oslo, P.O. Box 1050, Blindern, 0316 Oslo, Norway*

[5]*Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), José Gutiérrez Abascal 2, E-28006 Madrid, Spain*

[6]*Behavioural Ecology Group, Dept.Syst.Zool.& Ecol., Eötvös University, H-1117, Budapest, Pázmány P. sétány 1/C., Hungary*

[7]*Department of Biology, University of Oslo, P.O. Box 1050, Blindern, 0316 Oslo, Norway*

The pied (*Ficedula hypoleuca*) and the collared flycatcher (*F. albicollis*) hybridize and compete for resources in areas of sympatry. Evidence suggest a role of male song in territorial defence, mate attraction and species recognition. We compared song characters and song elements of flycatchers from four allopatric and two sympatric populations. In sympatry, the song of the pied flycatchers has converged towards that of the collared flycatcher. However, the species differences in song characters are maintained in sympatry because of a corresponding divergence in the collared flycatcher. Genetic analysis suggests that the song convergence in pied flycatchers is due to heterospecific learning rather than introgression from the collared flycatcher. A sympatric character divergence in plumage traits of these flycatchers has previously been shown to reinforce premating isolation. We suggest that reinforcement may similarly have operated on the song of sympatric flycatchers. Circumstantial evidence suggests that mixed singing increases the probability of hybridization. The frequency of mixed singing is much lower in the hybrid zones where reinforcement on plumage traits is most pronounced. Thus we suggest that reinforcement may have operated on song characters and song learning predispositions as a response to maladaptive hybridization.

28.9

SYMPATRIC SPECIATION FROM MUTUAL SEXUAL SELECTION

F Vistulo de Abreu, C. R. Almeida,

Universidade de Aveiro, 3810 Aveiro, Portugal

Department of Biological Sciences,Sir Alexander Fleming Building,Imperial College Science, Technology and Medicine,London SW7 2AZ, UK

One of the most challenging issues of evolutionary biology concerns speciation, the emergence of new species from an initial one. The huge amount of species found in nature demands a simple and robust mechanism. Yet, no consensus has been reached concerning a reasonable disruptive selection mechanism that prevents mixing genes among the emerging species, especially when they live in sympatry. Here we propose a new robust mechanism, based on the assumption that sexual selection operates in two directions: selection of males by females and of females by males. As a result complex mating instabilities emerge, creating differential fitness depending on the individuals displaying traits and preferences. When a secondary sexual trait is introduced in a population, due to mutations, the activation of previously neutral genes or due to a different perception of already existent displaying traits, sympatric speciation may result from a competitive exclusion principle. A discussion concerning the generality of the assumptions used will also be presented.

28.10

IMPLICATIONS OF MATE CHOICE FOR INBREEDING AND THE EVOLUTION OF SOCIALITY IN SPIDERS

[1]**Trine Bilde**, [2]Yael Lubin,

[1]*University of Aarhus, Department of Genetics and Ecology, Ny Munkegade Building 540, 8000 Aarhus C, Denmark*

[2]*Ben Gurion University, Mitrani Department of Desert Ecology, Sede Boker Campus 84990, Israel*

Evolution of sociality in spiders involves a transition from outbred mating systems in solitary species to inbred mating systems in social congeners. This transition is unusual in the animal kingdom, since most social animals maintain an outbred mating system by means of pre-mating or sex-specific dispersal. Outbreeding in solitary species can be maintained by discriminating against kin as mates or by male premating dispersal. We studied mate choice and male mating dispersal in closely related solitary and social species of *Stegodyphus* spiders (Eresidae). In the solitary *S. lineatus*, we found no behavioural discrimination against close kin as mates. Males had two distinct movement patterns with a proportion of males mating with genetically related mates within their neighbourhood, while others moved to distant neighbourhoods. Population genetic studies support this finding and suggest some degree of mating within sibling groups of *S. lineatus*. Inbreeding was tolerated, but F1 inbred offspring were smaller than outbred offspring. We suggest that fecundity selection in females and sexual selection in males, favour large body size and may thus act against inbreeding in *S. lineatus*. However, if costs of male dispersal are higher than costs of inbreeding, natural selection may favour inbreeding and elimination of costly mating dispersal. In social *Stegodyphus*, siblings remain in the natal nest and inbreed to produce subsequent generations. Male dispersal is highly reduced. We found that males of the social *S. dumicola* may move 5-6 m to mate with females in neighbouring colonies; however such colonies are genetically similar. Social *Stegodyphus* do not discriminate between mates from their own or foreign colonies, suggesting little or no selection for outbreeding. We propose that indiscriminate mate choice, high costs of dispersal and relatively low costs of inbreeding have promoted evolution of inbred social systems in spiders.

28.11

KIN RECOGNITION BASED FEMALE MATE DISCRIMINATION IN POLYANDROUS WASPS WITH AN INBREEDING SENSITIVE SEX DETERMINATION SYSTEM

[1]**Robert D. J. Butcher**, [2]Steve F. Hubbard, [2]William G. F. Whitfield

[1]*NERC Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berkshire, UK*

[2]*Department of Biology, Dundee University, Dundee, Tayside, Scotland*

Sexually reproducing organisms are expected to show a close association between sex determination mechanisms and mating systems. Single locus complimentary sex determination (CSD), a potentially ancestral from of arrhenotoky in the insect order Hymenoptera is common if not ubiquitous within the campoplegini tribe. Under CSD whilst unfertilised eggs develop as haploid males, fertilised eggs only develop as diploid females if heterozygous at the sex locus; homozygotes either are lethal or develop as (usually) sterile diploid males. Thus CSD is particularly sensitive to inbreeding with lose of half of the daughters. The chances of matched sex allele matings, and thus cost of CSD, can be reduced by selection for an increased number of sex alleles within large panmictic populations, but not small or frequently genetically bottlenecked populations. Therefore, species subject to CSD and frequent genetic bottlenecks should have evolved alternative mechanisms to mitigate the considerable fitness costs associated with inbreeding, assuming no evolutionary benefit to CSD. One such mechanism is discrimination against sex-allele-related mates. Parasitic wasps within the campoplegini tribe are subject to sl-CSD with sterile diploid males and often subject to genetic bottlenecks. Although polygamous, associative learning based kin, but not host or sex-allele related, female mate discrimination was found in two species (*Venturia canescens* and *Eriborus trochanteratus*), and supported by analysis of the observed frequencies of diploid males and matched mated females in small localised field populations and laboratory cages (3-5 sex alleles). In contrast, no evidence of mate discrimination at the level of copulation or sperm usage was found in all six wasps tested in the genus *Diadegma*. However, field estimates of matched mated females and diploid male frequencies in three of these species suggest mate discrimination is likely. Laboratory assessment of mate discrimination may be masked or insensitive in cases where semiochemical based associative learning is involved.

28.12

MATE CHOICE FOR OPTIMAL IMMUNITY

Joachim Kurtz, P. B. Aeschlimann, M. A. Häberli, M. Kalbe, T. B. H. Reusch, K. M. Wegner, M. Milinski

Max-Planck-Institute of Limnology, August-Thienemann-Str. 2, 24306 Ploen, Germany

Mate choice is based on immune genes in several animal taxa and in humans. However, in most cases, the functional consequences for the offspring remain obscure. A previous study showed that females of the three-spined stickleback (*Gasterosteus aculeatus*) prefer the odour of males that would sire offspring with an intermediate diversity in genes of the major histocompatibility complex (MHC). The MHC plays a central role in the modulation of the adaptive immune system. To test whether females would benefit from such a choice strategy in terms of offspring immunocompetence, we bred sticklebacks that varied in their individual number of different MHC molecules. As predicted, sticklebacks with intermediate MHC diversity suffered least from parasite infection after experimental exposure to tapeworms and microsporidians. Most interestingly, these fishes had the lowest proportion of granulocytes in relation to lymphocytes, together with lowest expression of an innate immune trait (the respiratory burst reaction). Our results suggest that the activity of the innate immune system can be reduced when the genetic diversity of the adaptive immune system is optimal, thereby potentially avoiding negative side effects of an overactive innate immune system. Our study suggests important evolutionary consequences of mate choice in species possessing an adaptive immune system.

28.13

MULTITUDE OF NON-ARBITRARY MALE SEXUAL ORNAMENTS IN THE LEKKING BLACK GROUSE

[1]**R. V. Alatalo**, [1]H. Siitari, [2]J. Hoglund, [2]A. Lundberg, [1]P. T. Rintamaki, [1]P. Halme, [1]J. Kilpimaa

[1]*University of Jyvaskyla, PO Box 35, FIN-40014 Finland*

[2]*Uppsala University, Villavagen 9, SE-75236, Uppsala, Sweden*

Many males have multiple ornaments, and female choice can base on several cues instead of only one cue. Many theoretical models assume that most of the multiple traits are Fisherian, and that only one handicap trait could exist in the same phenotype. However, the use of multiple cues could increase the costs for the females while at the same decreasing the errors in mate choice. In fact, black grouse has at least ten largely independent territorial, display or morphological signals. Here we show that the multitude of ornaments in the lekking black grouse honestly indicates male quality. Ornaments additively reflect male current and long-term condition, also effectively separating old individuals from young ones. The possible trade-offs between signals are weak or even absent, and top male have to express all the signals during the lekking time. Although male-male competition may drive the evolution of the multiple traits, female choice itself generates the evolution of informative ornaments in this species. Thus, here the multiple ornaments are likely to decrease the costs of mate choice for the females. Furthermore, this study indicates that several handicaps can evolve in the same male phenotype.

Posters

28.14P

TESTING FOR PARALLEL SPECIATION IN AFRICAN CICHLID FISH

Andrew M. Gould, Ole Seehausen, George F. Turner

Department of Biological Sciences, University of Hull, Hull, HU6 7RX, U.K.

Studies on stickleback fishes have raised the possibility that the same species can evolve multiple times in different places. Members of the *Maylandia zebra* species complex from Lake Malawi provide another possible example of this phenomenon. These fish inhabit rocky shores throughout the lake. Males are brightly coloured and attract females with a characteristic courtship ritual. Allopatric populations living in close proximity can differ in male colouration, and the same pairs of colour types can be found living close to each other in different parts of the lake. Phylogenetic studies based on microsatellite DNA indicate independent origins for populations bearing the same male colour but inhabiting opposite ends of the lake. However, it has yet to be shown that these independently-derived similar colour forms would interbreed in nature and thus be considered as members of the same biological species. Four populations differing in location and male dorsal fin colour were chosen. Populations with orange dorsal fins were collected from Mpanga Rocks in the North of the lake and Eccles Reef in the South; blue dorsal fin populations came from Nkhata Bay (N) and Chiofu Bay (S). To test for parallel speciation, we carried out four separate two-way comparisons, each population being compared with the neighbouring, different-coloured population and also with the geographically distant, same-coloured population. Females were presented with a selection of males with which they could spawn. Fertilised eggs were collected seven days after spawning and several microsatellite loci were analysed to determine paternity. Parallel speciation would be demonstrated if it was shown that same-colour populations interbred freely, while genetically more closely related different-colour populations did not.

28.15P

SYMPATRIC SPECIATION THROUGH SEXUAL SELECTION: DETERMINING THE GENETICS OF FEMALE MATING PREFERENCES IN LAKE VICTORIA CICHLID FISHES

M. Haesler, O. Seehausen

University of Hull, Biological Sciences, Hull, HU6 7RX, England

For mate choice to be evolutionary important it has to be heritable. Models about sympatric speciation make assumptions about the genetics of mating preferences. Especially in models where sexual selection is the driving force for species divergence, these assumptions have important consequences for the outcome of the models. To test these assumptions, we studied mate choice behaviour in a recently diverged cichlid species pair from Lake Victoria (East Africa). Given their distribution (Seehausen 1996), their morphological and ecological similarity (Seehausen and Bouton 1997) and their difference in male nuptial colouration which is the main cue for female mate choice (Seehausen and van Alphen 1998), we hypothesize that these two species have speciated in sympatry through sexual selection by female mate choice. Our experiments with the sister species *Pundamilia pundamilia* and *P. nyererei* (Cichlidae, Teleostei) and two generations of their hybrids suggest that female mating preferences are highly heritable. The mean female mating preferences of females of both hybrid generations were intermediate to those of females of the parental lines. Females of the F1 hybrid generation had no preference. Some F2 hybrid females showed a preference whereas some did not; they showed an almost continuous distribution of their mating peferences. These findings lead us to conclude that the female mating preference in *Pundamilia spp.* a) is inherited, b) is determined by more than one gene, and c) that there is no dominance of genes for preference for either colour.

28.16P

TACTICS OF MATE CHOICE AND THE EVOLUTION OF REPRODUCTIVE ISOLATION

Øistein Haugsten Holen, Glenn-Peter Sætre

Div. of Zoology, Dept.of Biology, University of Oslo, PO Box 1050 Blindern, N-0316 OSLO, Norway

Hybridization and mixed pairing often occurs in areas where one species is abundant and the other is scarce. It has been suggested that such interactions should occur more often between females of the rarer species and males of the common species than vice versa, because females are typically the more choosy sex, and because females of the rarer species would have relatively fewer conspecific mates to choose among compared to those of the common species. However, this prediction received equivocal or negative support in a recent meta-analysis of hybridization and mixed pairing among bird species. Here, we use simple models to discuss this apparent discrepancy in the light of mate search and speciation theory. We focus on how mate search strategies that are based upon sexually selected and continuously varying traits may affect reproductive isolation and patterns of mixed mating, and on conditions that may facilitate the evolution of species recognition per se.

28.17P

SOCIALLY MEDIATED SPECIATION

Michael Hochberg, Barry Sinervo, Sam P. Brown

University of Montpellier II, ISEM, CC065, 34095 Montpellier, France

We employ a simple model to show that social interactions can lead to pre-zygotic reproductive isolation via sexual selection. The evolution of social discrimination causes the congealing of phenotypically similar individuals into different, spatially distinct tribes. Tribal formation is only obtained, however, for certain types of social behavior: altruistic and selfish acts can produce tribes, whereas spiteful and mutualistic behaviors never do. Moreover, reduced hybrid fitness at tribal borders leads to the selection of mating preferences, which then spread to the core areas of the respective tribes. Unlike models of resource competition, our model generates reproductive isolation in an ecologically homogeneous environment. We elaborate on how altruistic acts can lead to reproductive isolation, but also predict that certain types of competition can lead to the speciation effect. Our theory provides a framework for how individual-level interactions mold lineage diversification, with parapatric speciation as a possible end product.

28.18P

FITNESS CONSEQUENCES OF FEMALE CHOICE IN LAKE VICTORIA CICHLID FISH

[1]Martine Maan, [2]Ole Seehausen, [1]Michael van der Spoel, [3]Linda Soderberg, [1]Kees Fofker, [1]Jacques van Alphen

[1]*Leiden University, Animal Ecology, PO Box 9516, 2300 RA Leiden, The Netherlands*

[2]*Department of Biological Sciences, University of Hull, Hull, HU6 7RX, U.K.*

[3]*Dept. of Animal Ecology, Uppsala University, Norbyvägen 18d, SE-752 36 Uppsala, Sweden*

The great lakes of East Africa, in which cichlid fishes have radiated into hundreds of coexisting species, present an ideal system to study the mechanisms of speciation and the processes governing species diversity. Lake Victoria is the youngest of these lakes, yet it harbours an extremely diverse haplochromine fish fauna, consisting of over 500 species.

Several observations suggest that both male and female choosiness with regard to body coloration of potential mates can exert diversifying selection upon coloration. However, the selection forces that shape mate choice (hence the fitness consequences of mate selectivity to the chooser) are still largely unknown.

We investigate fitness correlates of body coloration and the fitness consequences of mate choice based on variation in body coloration. We focus on a species in which females prefer bright red males, *Pundamilia nyererei*. If female choice is adaptive, it must select for good genes rather than direct benefits, since males do not contribute to brood care at all. Behavioural observations in the field and in the lab together with quantitative analysis of male colour and parasite load suggest that female choice indeed selects for heritable quality: red coloration signals parasite resistance.

28.19P

FEMALE BURYING BEETLES PREFER SMALL SERVILE MALES

Allen J. Moore, V. Tamara Montrose, Judith E. Lock, Melanie Gibbs, Per T. Smiseth

School of Biological Sciences, University of Manchester, Oxford Road, Manchester M13 9PT

Burying beetles have unusually well-developed parental care for insects. Males as well as females feed and care for developing young, although females provide most of the direct care to offspring. We examined whether females discriminated among males when provided a choice. When male-male competition was experimentally eliminated, females preferentially mated with smaller males over larger males, even when males were associated with the resources needed for reproduction by females. We also examined the fitness consequences of female preferences. When females mated with preferred males, the offspring produced developed faster and were larger than offspring produced when mated to an unpreferred male. Other research by our group suggests that female preferences for smaller males are likely to reflect a preference for reduced (male) parent-offspring competition for resources.

28.20P

PARASITES MAKE MALE PIPEFISH CARELESS

Dominique Mazzi

University of Oulu, Dept of Biology, PO Box 3000, 90014 Oulu, Finland

Models of parasite-mediated sexual selection predict that individuals should avoid matings with parasitized partners. However, the extent to which the costs and benefits of discriminating against parasitized mates trade off may depend upon numerous factors. I investigated the effects of sex and infection status on choosiness in male and female deep-snouted pipefish (*Syngnathus typhle* L.) that were either artificially infected with the trematode parasite *Cryptocotyle* sp. or sham-infected. In simultaneous mate choice tests, sham-infected males were significantly more likely to associate with a sham-infected female rather than with an artificially *Cryptocotyle*-infected female. Infected males, on the contrary, failed to discriminate against infected potential partners. Males were choosier the fewer parasites they harboured and the larger they were relative to the female stimuli. Females were not discriminatory, regardless of their own infection status. Given an inverse relation between female fecundity and parasite load, choosy unparasitized males may gain enhanced reproductive success from their choice decisions. In contrast, more heavily infected wild-caught males gave birth to slightly fewer, but not smaller offspring than did uninfected or lightly infected males, suggesting only a low direct premium on choosy females. The detrimental effects of parasites on male choosiness, and the lack of female discrimination against infected males likely have profound repercussions on the strength of sexual selection acting on the two sexes, as well as on the dynamics of host-parasite interactions in this system.

28.21P

GENOTYPE-ENVIRONMENT INTERACTIONS OF SEXUALLY SELECTED TRAITS

S. C. Mills, E. Koskela, T. Mappes, T. Oksanen

University of Jyväskylä, P.O. Box 35 YAC, FIN - 40014, Jyväskylä, Finland

Studies on evolutionary consequences of sexual selection assume that sexually selected traits are highly heritable. However, studies on sexual selection widely ignore that the performance of different genotypes vary with environmental conditions. Male mating quality was compared among bank voles (*Clethrionomys glareolus*) that were exposed to different environmental conditions during growth. Offspring were cross-fostered and weaned in experimentally manipulated litter sizes. The growth of bank vole pups in enlarged, control and reduced litter sizes corresponded to poor, unchanged and good growth conditions respectively in terms of body mass and head width at weaning. We found evidence for stabilising selection on litter size, such that offspring from unchanged litter sizes had higher fitness in terms of mating quality, than offspring from reduced and enlarged litter sizes. We then compared the heritability of male mating quality among the different growth environments. Although there is an additive genetic component of male mating quality, only offspring under good growth environments showed a high heritability estimate for mating quality. We will discuss how different additive genetic components in different environmental conditions might significantly affect the strength of stabilising selection.

28.22P

MALE PHENOTYPE AND PATERNITY IN THE GUPPY

Alfredo F. Ojanguren, Anne E. Magurran

University of St Andrews, Gatty Marine Laboratory, KY16 8LB St Andrews, Scotland, U.K.

The Trinidadian guppy (*Poecilia reticulata*) has a truly promiscuous mating system. Males, which spend most of their time pursuing females, have two methods of securing inseminations. They may either solicit a consensual mating with a receptive female using the sigmoid display, or engage in sneaky mating and attempt to copulate with unreceptive females. All males use both tactics. However, despite extensive research on guppy mating behaviour, the relative importance of these tactics remains unknown. In this study we explored a number of aspects of male phenotype that could explain the observed variability in male reproductive success, defined as the number of offspring fathered. The experiment had 12 replicates, each with 4 males and 4 females. Male behaviour was recorded by observing focal males during 10-minute periods. Each male was observed 23 times during the 34 days that the experiment lasted. Male size and coloration were measured from a digital image. Females were kept in individual tanks until they gave birth. The juveniles were then collected for genetic analysis. Forty-eight males, 40 females and 206 juveniles were genotyped using three highly variable guppy-specific microsatellite loci. Paternity analysis revealed high levels of multiple paternity (23 out of 40 broods had more than one father) and a marked variability in male success (from 0 to 13 offspring). Individual male behaviour was consistent throughout the experiment, and within male variance in mating activity was lower than among male variability. However, contrary to our predictions, male mating behaviour was not a good predictor of male reproductive success.

28.23P

MARRY THE BOY NEXT DOOR OR LOOK FURTHER? HETEROSIS AND OUTBREEDING DEPRESSION IN PRE-INDUSTRIAL HUMAN POPULATIONS

[1]Jenni Pettay, [2]Virpi Lummaa

[1]University of Turku, Section of Ecology, Department of Biology, FIN-20014, Turku, Finland

[2]Large Animal Research Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge, U.K.

By outbreeding, individuals may enhance the success of their (F1) offspring through heterosis. The second generation (F2), however, seldom benefits from heterosis, and may even suffer from outbreeding depression. We studied heterosis and outbreeding depression in humans in four pre-industrial (1740-1860) Finnish populations using individual-based demographic records (n=1,895) documenting life-history for three full generations (P, F1, F2). During the study era, the population was mostly rural, population densities were low and approximately 90% of individuals married within their natal village. This isolation by density led to small local breeding units, enabling us to use geographic distance between spouses birth parishes as a measure of relatedness. We compared survival and lifetime reproductive success in P, F1 and F2 generations in (1) lines in which the parental generation individuals married within their natal parish and (2) lines in which the parents chose their spouse from further away. Our results show that there were no overall fitness differences in parental generation. However, parental outbreeding benefited F1 generation female offspring by improved offspring survival and altogether higher lifetime reproductive success. We found no evidence of similar benefits among F1 males. However, fitness benefits were lost in following F2 generation. These results were further compared between areas with historically small breeding units and more outbred areas.

28.24P

SPECIATION BY SELECTION ON SEX REVERSAL AND SEXUAL SELECTION: THE ROLE OF MALE MATING PREFERENCES

Michele Pierotti, Ole Seehausen

Department of Biological Sciences, University of Hull, Hull, HU6 7RX, U.K.

A polymorphism in mate preferences may cause strong premating isolation in sympatry leading to rapid sympatric speciation with very small genome-wide differentiation and initially little or no morphological or ecological divergence. The explosive radiation of cichlid fishes in the Lake Victoria basin provides an ideal model system to test this hypothesis. More than 500 closely related species have radiated from one or a few ancestors with similar colour polymorphisms recurring across many taxa and there is evidence that mate choice based on colour patterns is the major isolating mechanism among sympatric species.

Recent theoretical work has shown that multiple speciation events can occur when a combination of sexual selection by mutual mate choice and sex ratio selection is involved. The mechanism considers the invasion of an X-linked dominant female determining, and hence sex ratio distorting gene (W) in a population. A new colour gene linked to W could then spread because, being restricted to females, it would not be exposed to negative sexual selection by female choice. In a population that has some variation in strength of male sex determiners and mating preferences, segregation of such a gene can exert selection dynamics that lead to sympatric speciation.

The existence, direction and strength of male and female mate preference are crucial for this mechanism of sympatric divergence. In particular, a strong mate preference in ancestral type males against the novel colour is required. We conducted focal observations of male courtship behaviour and molecular paternity typing of eggs in two unrelated Lake Victoria cichlid species with a colour-marked W/X/Y chromosome polymorphism i) to test for male mating preference, ii) to explore the association between male preference and male sex genes and ii) to test whether behavioural male mating preferences would translate in assortative mating in a semi-natural setting.

In *Neochromis omnicaeruleus* three male and female colour morphs occur sympatrically. Previous studies have suggested that this polymorphism represents one original species and two incipient species connected to the ancestral one by unidirectional gene flow.

In *Paralabidochromis chilotes*, females from two allopatric populations are fixed for alternative colour patterns, closely resembling the *N. omnicaeruleus* polymorphism. Since males have identical colour patterns in the two populations, it is possible to isolate the effects of male from female mating preferences and test the prediction that ancestral type males have preferences against the novel female morph. Preliminary results suggest strong male mating preference and assortative mating occurring between *P. chilotes* populations that only differ in female colour/sex gene morph. The *N. omnicaeruleus* population is variable for male mating preferences with some males of the ancestral colour showing strong preference against the novel female colour, but others not; moreover, males of the novel morph exhibit mate preference against the ancestral female morph.

28.25P

FEMALE COLLARED FLYCATCHERS LEARN TO PREFER MALES WITH AN ARTIFICIAL NOVEL ORNAMENT

A. Qvarnström, V. Blomgren, C. Wiley, N. Svedin

Dept. of Animal Ecology, Uppsala University, Norbyvägen 18d, SE-752 36 Uppsala, Sweden

We experimentally investigated whether learning from previous experiences can lead to the establishment of a new mate preference in a wild population of birds. During year one (2001), 63 female collared flycatchers (*Ficedula albicollis*) bred together with males that we had provided with a novel trait, a red stripe on their white forehead patch (a sexually selected trait). Some colour patterns of birds are largely determined by a few genes and this experiment was designed to mimic the occurrence of mutations in such genes. In the subsequent year (2002) we found that females with previous experience of red-striped males were more likely to pair to red-striped males (76%) than to control males. By contrast, naïve females (i.e. with no previous experience of red-striped males) were not more likely to pair to red-striped males (44%) than to control males. Females paired with red-striped males produced more offspring than females paired with control males suggesting that males with the novel trait had become favoured by selection. Thus, female collared flycatchers appear to quickly learn to associate a novel trait with a suitable mate that, in turn, leads to assortative mating between local mates (i.e. males with the new trait and females with previous experience of the new trait). Our results provide support for the notion that learning may play an important role when the co-evolution between preferences and preferred traits takes different routes in different populations of the same bird species.

28.26P

VARIATION IN MALE AND FEMALE REPRODUCTIVE SUCCESS IN A WILD AMPHIBIAN POPULATION

Dirk S. Schmeller, David Lesbarreres, Craig Primmer, Juha Merilä

University of Helsinki, Ecological Genetics Research Unit, Department of Ecology and Systematics,Biocenter 3, 00014 Helsinki, Finland

Individual variation in reproductive success is an important quantity in evolutionary biology as it determines the opportunity for natural and sexual selection. It is also an important quantity in population genetics as the variation in reproductive success influences the effective size of the population. To date, our understanding of causes and consequences of individual variation in reproductive success in the wild have been mostly confined to avian and mammalian systems where quantification of reproductive success is relatively easy. In contrast, estimates of individual variation in reproductive success in amphibians are rare as the assigment of offspring to their putative parents is not possible without access to highly variable molecular markers. We utilized eleven microsatellite loci to determine variation in male and female reproductive success in two breeding ponds of the common frog, *Rana temporaria*. By assigning all surviving metamorphs to their parents, we were able to quantify the variation in actual reproductive success among 140 adult individuals, as well as natural selection acting on adult traits.

28.27P

THE IMPORTANCE OF FEMALE ORNAMENTS IN BLUE TITS

Heli Siitari, Rauno Alatalo, Satu Kuntsi

University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35 (YAC442), FIN-40014 Jyväskylä

Mate choice is commonly based on sexually selected characters (secondary sexual traits). Studies on secondary sexual traits have focused almost solely on males, although the females of many species among fish, mammals and birds are also ornamented. Only recently it has been debated that female ornaments are not only genetically correlated by-products of selection on males, but could be also sexually selected e.g. through male choice or female-female competition. In this study, we investigated the importance of coloration as a signal of female quality in monogamous blue tits *Parus caeruleus*. In a field study, we investigated assortative mating and the relationship between several quality parameters (e.g. timing of breeding, parasite load, clutch size, offspring sex ratio and condition) and coloration (structural- and carotenoid-based coloration). In two aviary experiments, we investigated the importance of female ornamentation in female-female competition within young female blue tits in February 2003. The first experiment was carried out with natural coloration, and in the second experiment we manipulated the UV chroma of the females. The field study indicates that the pairing is assortative with respect to structural-based coloration. Furthermore, the individuals (both males and females) with a higher colour parameter (UV chroma) are less likely to carry parasites. The preliminary results of the aviary experiments indicate, that the UV chroma of females does not indicate female dominance, but the brightness of the ornament, as well as some other colour parameters are related to dominance rank. However, the manipulation of UV chroma itself did not affect the final rank of females, but the preliminary results indicate that the reduction of UV chroma increased the aggression between experimentally reduced and control females. The results support the recent finding that male choice in blue tits could work also in natural population and generally, female ornaments can be related to female quality.

28.28P

ARE GENES FOR MATE PREFERENCE AND GENES FOR COLOUR PHYSICALLY LINKED IN RAPIDLY SPECIATED LAKE VICTORIA CICHLID FISHES?

[1]Inke Van der Sluijs, [2]Ole Seehausen, [1]Jacques, J. M. Van Alphen

[1]*Leiden University, Animal Ecology, PO Box 9516, 2300 RA Leiden, The Netherlands*

[2]*Hull University, Molecular & Evolutionary Ecology Group, Hull HU6 7RX, United Kingdom*

The cichlid fishes of Lake Victoria are known for their enormous diversity and rapid speciation, but the mechanisms underlying this rapid speciation are still unclear. Sexual selection through female choice for male colour has been raised as a possible explanation. The two species studied here, *Pundamilia pundamilia* (blue males) and *Pundamilia nyererei* (red males), could have arisen by co-evolution of mate preference and colouration. The genetic mechanism could either be selective mating having led to, and now maintaining linkage disequilibrium between genes or physical linkage between preference and colour genes. We want to test the physical linkage by mate choice experiments. We have hybridised *P. pundamilia* and *P. nyererei* and mated the F1 offspring to obtain an F2 generation. The preference of hybrid female F2 offspring will be tested in mate choice experiments. Five F2 females on one end of the distribution with preference for blue will be crossed each with one blue (since red is semi-dominant) male of the lab stock with a known genetic background. One of the five F2 females on the other end of the distribution with preference for red will be allowed to mate with each one of the same blue males. If preference and colour are physically linked, the male F3 offspring of the blue-preferring females should be more blue than that of the red-preferring females. The colour of the offspring will be quantitatively analysed. If we do not find evidence for physical linkage, selection as a cause of linkage disequilibrium in nature despite hybridization has to be investigated.

28.29P

DOES INBREEDING AFFECT SEX ALLOCATION IN THE ANT *FORMICA EXSECTA?*

Emma Vitikainen, Cathy Liautard, Liselotte Sundström

University of Helsinki, Institute of Ecology and Systematics, PO Box 65, 00014 Helsinki, Finland

The rate of habitat fragmentation caused by human activities is accelerating with severe consequences for animal life history traits such as dispersal and breeding patterns. It will increase the risk of inbreeding, and potentially the rate of inbreeding depression. In social insects the consequences of inbreeding may be different to those observed in other taxa, since selection may act on both individual and colony level. Previous data have shown that in single-queen colonies of *Formica exsecta*, workers are inbred to the extent that approximately 40% of them are the offspring of brother-sister matings, whereas no significant inbreeding was found in resident queens. As workers and queens are issued from the same batch of diploid eggs, this suggests selection against inbred queens. This difference in inbreeding between the two castes of diploids could arise in two ways. First, young inbred queens may have lower fitness and may therefore be less successful during colony foundation (see abstract by Liautard et al.). Second, colonies producing inbred offspring can specialise in producing mainly male sexual offspring. In the study population of *Formica exsecta* sex ratios are split so that approximately half of the nests produce only male, and the other half female sexual offspring. Queen mating frequency has been shown to have an effect on colony sex ratios. As inbreeding level of offspring might be tightly linked to mating frequency, we compared inbreeding level between male and female producing nests to see if inbreeding is correlated to sex allocation and mating frequency in those colonies.

Symposium 29

Evolutionary dynamics of the major histocompatibility complex (MHC)

Organisers: Stuart Piertney & Steve Paterson

Conference Auditorium 2

9.50 - 10.20	**Hedrick, P.** Selection at MHC: General perspective and estimation in salmon and humans
10.20 – 11.00	**Coffee**
11.00 – 11.30	**von Schantz, T.** Defence systems, MHC and radical sexual signals
11.30 – 12.00	**Potts, W. K.** Pathogen-mediated selection acting on histocompatibility genes
12.00 – 12.20	**Surridge, A. K.** MHC diversity and reproductive success in wild European rabbits (*Oryctolagus cuniculus*)
12.20 – 12.40	**Palmén, A.** Spatial heterogeneity in MHC polymorphism and intensity of multiple parasite infection in Arctic charr
12.40 – 14.00	**Lunch**
14.00 – 14.20	**Westerdahl, H. W.** Between-year variation of MHC allele frequencies in great reed warblers: selection or drift?
14.20 – 14.40	**Piertney, S. B.** MHC diversity, disease resistance and mate choice in red grouse (*Lagopus lagopus scoticus*)
14.40 – 15.00	**Reusch, T. B. H.** Divergent selection at MHC Class IIB genes across locations with contrasting parasite communities
15.00 – 15. 20	**Ekblom, R.** MHC class II variation and mate choice in a lekking bird, the great snipe (*Gallinago media*)
15.20 – 16.00	**Tea**

Invited talks

29.1

SELECTION AT MHC: GENERAL PERSPECTIVE AND ESTIMATION IN SALMON AND HUMANS

Phil Hedrick, Dan Garrigan

Department of Biology, Arizona State University, Tempe, AZ 85287, USA

Genes in the MHC are prime examples of adaptive evolutionary change. However, inference of selection from tests based on molecular patterns should be made carefully, particularly when considering the timing of selection. Overall, the time necessary to generate selective signals is much less than the time necessary to lose these selective signals. The maintenance of MHC variation is generally thought to be the result of adaptation to pathogens and a model for this interaction will be introduced. A direct test of the differential selection at a MHC gene in salmon for two different pathogens will be discussed. Finally, MHC and microsatellite variation in a human population that has been through both a bottleneck and suffered from infectious diseases will be presented. Overall, the microsatellite data indicate the bottleneck impact and the MHC data suggest an additional impact, presumably due to selection related to disease. Even for paradigmic selective genes such as those in the MHC, demonstrating the mode and impact of selection requires thoughtful and intensive research.

29.2

DEFENCE SYSTEMS, MHC AND RADICAL SEXUAL SIGNALS

Torbjörn von Schantz

Department of Animal Ecology, Lund University, S-223 62 Lund, Sweden

The immune and the detoxication system of animals are characterised by allelic polymorphisms which underlie individual differences in abilities to combat assaults from pathogens and toxic compounds. Previous studies have shown that allelic variants in these defence systems affect indivual health and fitness. Activated immune and detoxication systems often generate oxidative stress by an extensive production of reactive metabolites and free radicals. In many cases the expression of condition-dependent sexual ornaments appears to be particularly sensitive to oxidative stress. Given that tolerance or resistance against toxic compounds and pathogens can be inherited, female choice should promote the evolution of male ornaments that reliably reveal the status of the bearers' level of oxidative stress. Hence, oxidative stress may be one important agent linking the expression of sexual ornaments to genetic variation in fitness-related traits thus promoting the evolution of female mate choice and male sexual ornamentation.

29.3

PATHOGEN-MEDIATED SELECTION ACTING ON HISTOCOMPATIBILITY GENES

Wayne K. Potts, Erin E. McClelland

Department of Biology, University of Utah, Salt Lake, UT 84112, USA

Major histocompatibility complex (MHC) genes control immunological self/nonself recognition and are the most diverse genes known in vertebrates. Despite the importance of these genes to biomedical traits such as tissue rejection, tumor surveillance, and susceptibility to infectious and autoimmune diseases, we still do not understand the biological significance of MHC diversity. Here we report results from experimental tests for the two leading pathogen-based explanations for MHC genetic diversity. First, MHC heterozygote superiority might emerge over multiple infections because MHC-mediated resistance is generally dominant and many allele-specific susceptibilities to pathogens will be masked by the resistant allele in heterozygotes. We tested this hypothesis using experimental coinfections with *Salmonella enterica* and Theiler's murine encephalomyelitis virus (TMEV) in MHC-congenic mouse strains where one haplotype was resistant to *Salmonella* and the other was resistant to TMEV. MHC heterozygotes were superior to both homozygotes in 7 out of 8 comparisons ($P<0.0024$), and the mean standardized pathogen load of heterozygotes was reduced by 41% over that of homozygotes ($p<0.01$). In contrast, no heterozygote superiority was observed when the MHC haplotype combinations had similar susceptibility profiles to the two pathogens. This is the first experimental demonstration of MHC heterozygote superiority against multiple pathogens. Second, MHC polymorphisms may be the result of rapidly evolving pathogens adapting to (evading) MHC-dependent immune recognition, thereby generating cycles of frequency-dependent selection. This hypothesis assumes that pathogens can evade MHC-dependent immune recognition of their hosts. We tested this assumption by passaging the pathogenic fungus *Cryptococcus neoformans* through each of four different MHC-congenic mouse strains for approximately 400 pathogen generations during 9 passage cycles. Virulence increased insignificantly in the k haplotype, at intermediate levels in b ($p=0.08$) and f ($p=0.05$) haplotypes and dramatically in Balb/C and the q haplotype ($p<0.001$). Although MHC influenced the trajectory of virulence evolution, the majority of virulence increase was MHC-independent. Both of these pathogen-based mechanisms would contribute to MHC genetic diversity. However, evaluating their relative importance will be difficult because both depend on the interactions of all infectious agents experienced by hosts over their lifetime.

Contributed talks

29.4

MHC DIVERSITY AND REPRODUCTIVE SUCCESS IN WILD EUROPEAN RABBITS (*ORYCTOLAGUS CUNICULUS*)

Alison K. Surridge

University of East Anglia, Norwich, UK

Mate choice has been implicated as a possible mechanism for promoting genetic diversity in the Major Histocompatibility Complex (MHC). Behaviours whereby individuals select mates based on their MHC genotype could be adaptive when they provide their offspring with a more diverse molecular repertoire to respond to challenges by pathogens or disease. The European wild rabbit (*Oryctolagus cuniculus*) provides an ideal model for investigating such mechanisms that promote MHC polymorphism. Living in stable social groups, olfactory processes are important for determining social and reproductive status, and in mate choice. Strong selective forces are applied to rabbit populations in the form of the myxoma virus, which can be responsible for mortality of up to 80%. Here we describe levels of MHC polymorphism in a wild rabbit population which has been intensively studied for over 20 years and is subject to predictable annual myxomatosis epidemics. Parentage analysis of young rabbits is performed, giving a measure of reproductive success of different pairings based on MHC genotype. The importance of mate choice and disease in promoting MHC diversity in wild rabbits is discussed.

29.5

SPATIAL HETEROGENEITY IN MHC POLYMORPHISM AND INTENSITY OF MULTIPLE PARASITE INFECTION IN ARCTIC CHARR

[1]**Andreas Palmén,** [2]Ståle Liljedal, [1]Mats Grahn, [2]Ivar Folstad

[1]*Södertörn University College, Dept. of Natural Sciences, SE-14189 Huddinge, Sweden*

[2]*University of Tromsø, Inst. of Biology, Dept. of Zoology/Ecology, NO-9037 Tromsø, Norway*

The extreme polymorphism found at some major histocompatibility complex (MHC) loci is believed to be maintained by balancing selection caused by infectious pathogens. Multiple parasite infection may influence the spatial heterogeneity in major histocompatibility complex polymorphism. Here we tested these ideas by screening wild populations of landlocked Arctic charr (*Salvelinus alpinus* L.) for the variation in MHC class *IIB*, using the denaturing gradient gel electrophoresis (DGGE) technique, and for the diversity and intensity of parasite infections. The exon 2 alleles, encoding the major part of the peptide-binding region, were established for each DGGE fragment. The parasite diversity and intensity may influence the distribution of different MHC class *IIB* alleles in the screened populations and affect the pattern of common and rare alleles that is observed. Our study presents support for the hypothesis that MHC polymorphism is mainly maintained through frequency dependent pathogen-driven selection. We did on the other hand not find any evidence for an overall heterozygote advantage.

29.6

BETWEEN-YEAR VARIATION OF MHC ALLELE FREQUENCIES IN GREAT REED WARBLERS: SELECTION OR DRIFT?

H. W. Westerdahl, B. Hansson, S. Bensch, D. Hasselquist

Lund University, Ecology Building, 223 62 Lund, Sweden

The major histocompatibility complex (MHC) has an important role in the immune defence of vertebrates where it recognises foreign peptides, and triggers immune responses. The MHC genes are extremely polymorphic and this variation is assumed to be maintained by balancing selection. Cyclic interactions between pathogens and their hosts could generate such selection, and specific MHC alleles or heterozygosity at certain MHC loci have been shown to confer resistance against particular pathogens. Here we compare the temporal variation in allele frequencies of MHC class I genes with that of neutral microsatellite markers in adult great reed warblers in nine successive cohorts. We investigated 23 MHC alleles and compared the observed pattern with the variation of a similar number of randomly picked microsatellite markers. The analyses showed that the frequency of two MHC alleles, A3e ($p = 0.046$) and B4b ($p = 0.0018$), varied more between cohorts than expected from random, whereas none of the microsatellite alleles did so. In total, six MHC alleles varied more between cohorts ($p = 0.0018$-0.11) than did the most variable microsatellite allele (p ³ 0.17). These results imply that the variation in MHC allele frequencies between great reed warbler cohorts is not a result of demographic events, but rather an effect of selection favouring different MHC alleles in different years. A possible explanation for this remarkable variation is that pathogens vary considerably in space and time exposing different cohorts to different pathogen regimes.

29.7

MHC DIVERSITY, DISEASE RESISTANCE AND MATE CHOICE IN RED GROUSE (*LAGOPUS LAGOPUS SCOTICUS*)

Stuart B. Piertney

School of Biological Sciences, University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, UK

The high levels of allelic diversity observed at MHC genes have been attributed to the effects of balancing selection mediated through host-parasite co-evolution and/or disassortative mating and sexual selection. Here I examine the relative contributions of these processes to the diversity of Class IIB (avian B-LB) genes in red grouse. Each grouse holding a territory at Glas Choille moor (NE Scotland) between 1994 and 2002 was sampled, and the DNA sequence of the second exon of the class II beta MHC gene determined. The ratio of non-synonymous:synonymous substitutions at sites coding for the peptide binding region was ascertained to confirm the effects of balancing selection. The influence of MHC on mate choice was determined by: 1) comparing the frequency of heterozygote offspring relative to Hardy-Weinberg expectations; 2) directly comparing the MHC type of paired individuals. Association between MHC type and parasite burden was examined by determining: 1) if a particular allele or locus heterozygosity was associated with low parasite burden after controlling for age, size, sex, etc; 2) if allele frequencies changed over time in response to changing parasite load.

29.8

DIVERGENT SELECTION AT MHC CLASS IIB GENES ACROSS LOCATIONS WITH CONTRASTING PARASITE COMMUNITIES

Thorsten B. H. Reusch, K. M. Wegner, M. Kalbe

Max-Planck-Institute of Limnology, August-Thienemann-Str. 2, 24306 Ploen, Germany

Whether or not population differentiation at MHC genes is mainly driven by neutral genetic processes or by selection is still an open question. Comparisons between genetic differentiation at neutral loci (microsatellites) and MHC loci using frequency based approaches have been inconclusive because the misfit in the correlation between MHC and microsatellite allele frequencies necessary to reject the null hypothesis is difficult to quantify. As a second problem, the relevant selection pressures for MHC genes (i.e. parasites) often remained undefined. In recently diverged populations of three-spined sticklebacks (*Gasterosteus aculeatus*) in northern Germany we also find a close correlation between genetic differentiation at microsatellite and MHC class IIB loci. This was surprising since stickleback populations from rivers, lakes and estuaries are infected by markedly distinct parasite assemblages. We show that the signal of divergent selection becomes detectable when focussing on specific features of the MHC class IIB alleles at the sequence level. In a set of of 66 exon 2 sequences from three populations (one per habitat type) we tested whether base substitution patterns leading to amino acid change (=non-synonymous substitutions) were biased towards more inter-population divergence. In accordance, there were on average more substitutions at replacement sites between sequence pairs belonging to different populations than expected by chance alone. When only base substitutions within codons homologous to antigen presentating codons in humans were considered, inter-population divergence was 10 - 60 times higher than the mean random value, and significant in a permutation procedure. Our data suggest a role of selection in promoting the divergence at MHC class IIB sequences between populations, in particular at functional positions involved in antigen recognition, indicating different selection pressures mediated by parasites.

29.9

MHC CLASS II VARIATION AND MATE CHOICE IN A LEKKING BIRD, THE GREAT SNIPE (*GALLINAGO MEDIA*)

[1]**R. Ekblom**, [2]S. A. Sæther, [3]M.Grahn, [1]J. Höglund

[1]*Population Biology/Evolutionary Biology Centre, Uppsala University, Norbyv.18D, SE-752 36 Uppsala, Sweden*

[2]*Evolutionary Biology/Evolutionary Biology Centre, Uppsala University, Norbyv.18D, SE-752 36 Uppsala, Sweden*

[3]*Södertörn University College, Box 4101, SE-141 04 Huddinge, Sweden*

In some species mate choice is influenced by MHC (Major Histocompatibility Complex) variation. The MHC molecules are responsible for presenting antigen peptides to the immune system, leading to triggering of the immune response. It has been proposed that females choose to mate with a male that has a different set of MHC-genes than herself in order to give the offspring a large set of alleles resulting in a broad defence against many kinds of parasites. We have investigated MHC class II variation and mating patterns in a migrating wader, the great snipe. This species has a lek mating system, where males gather at arenas to display and compete for mating opportunities. The females visit the leks for the sole purpose of mating and then takes care of the incubation of the clutch by herself. The males do not contribute any resources except genes to the offspring. This system is thus suitable for studying possible MHC-effects on mate choice. The study is based on data from two leks that have been monitored for several years. Colour ringed individuals have been followed and visits, solicitations and matings have been recorded. We have collected blood samples from both males and females. Polymorphism in the second exon of MHC class II genes have been investigated using denaturing gradient gel electrophoresis (DGGE) and sequencing. We address whether females mate with males that have a different MHC-haplotype compared to their own.

Posters

29.10P

MAJOR HISTOCOMPATIBILITY COMPLEX VARIATION IN SMALL POPULATIONS OF BROWN TROUT (*SALMO TRUTTA*)

Jose Luis Campos-Parada, David Posada, Paloma Morán

Departamento de Bioquímica, Genética e Inmunología. Campus Lagoas Marcosende. Universidad de Vigo. Vigo 36200. Spain

Genetic variation at the major histocompatibility complex (MHC) class II B locus was examined in nine brown trout populations inhabiting the Sella river drainage of Asturias (North Spain). The nine populations are isolated from each other and no contact among these populations or others is allowed due to natural barriers. Local people have introduced six of the populations at the beginning of the XX century in the area of Picos de Europa where natural populations were not present. The remaining three are healthy natural populations inhabiting small streams and therefore the have small population sizes. Genetic analysis at four microsatellite loci revealed no variation or very poor variation in seven of the analyzed populations. Further genetic variation was investigated at MHC locus, due to the characteristics and function of these genes that are some of the most variable in vertebrates. Balancing selection is the responsible of the maintenance of the polymorphism levels and the persistence of individual alleles, the relationship among these populations belonging to the same drainage were also analyzed. More than 23 alleles were found in the 280 individuals analyzed. Five of the populations where monomorphic (four introduced, one natural) and the remaining four account for most of the variation. Very few alleles where shared among populations. In general terms not variable populations at microsatellite loci were not variable at the MHC analyzed sequence where as more polymorphic populations at microsatellite loci are the more polymorphic at MHC locus. With respect to comparison of the different MHC alleles, 64? out of the 257 position were variable. A high rate of dN/dS was detected indicating positive selection, especially in positions that may be related to peptide-binding regions (PBR). In addition, there was evidence of intrallelic recombination.

29.11P

POLYMORPHISM IN THE MHC CLASS IIB OF THE RED-BILLED GULL (*LARUS NOVAEHOLLANDIAE SCOPULINUS*)

[1,2]Nicola L. Chong, [1]Alessandro Grapputo, [3]James A. Mills [1]Allan J. Baker

[1]Centre for Biodiversity and Conservation Biology, Royal Ontario Museum, ON, Canada

[2]Dept. Zoology, University of Toronto, ON, Canada

[3]5 Skyline Drive Corning, NY

The avian major histocompatibility complex appears to vary considerably among species. To investigate the evolution of the MHC class IIB gene region we have used SSCP analysis, cloning and sequencing of alleles from 8 family groups of Red-billed gulls. The sequenced alleles likely come from at least two different loci. The amino acid substitutions in the second exon follow the general pattern of high non-synonymous to synonymous substitution rates suggesting that the alleles are from functional genes. Phylogenetic analysis shows that the MHC class II B of the Red-billed gull is most closely related to the MHC class II of Great snipe (*Gallinago media*), supporting previous findings that Charadriiform MHC organization is intermediate between Galliformes and Passeriformes.

29.12P

THE USE OF REFERENCE STRAND-MEDIATED CONFORMATIONAL ANALYSIS IN THE STUDY OF CHEETAH (*ACINONYX JUBATUS*) MHC CLASS II VARIABILITY

[1]Gabby Drake, [2]Lorna J. Kennedy, [1]Harriet Auty, [1]Ruth Ryvar, [3]Andrew C. Kitchener, [4]Abigail R. Freeman, [2]William E.R. Ollier, [1]Alan D. Radford

[1]University of Liverpool, Veterinary Teaching Hospital, Leahurst, Chester High Road, Neston, CH64 7TE, UK

[2]Centre for Integrated Genomic Medical Research, University of Manchester, Stopford Building, Oxford Road, Manchester, M13 9PT, UK

[3]National Museums of Scotland, Royal Museum, Chambers Street, Edinburgh EH1 1JF, UK

[4]Department of Genetics, Smurfit Institute of Genetics, Trinity College, DUBLIN 2, Ireland

There has been much debate about the degree of variation in the cheetah (*Acinonyx jubatus*) MHC (feline leucocyte antigen [FLA]) and its significance to population fitness. This debate has been hampered by the inability to rapidly type FLA-DRB, as demonstrated by recent studies using cloning and sequence analysis that are slow, expensive and always likely to underestimate true diversity. In this study we have applied Reference Strand-Mediated Conformational Analysis (RSCA) to determine the FLA-DRB phenotypes of 26 cheetahs. This technique was shown to be rapid, repeatable and less prone to the PCR-induced sequence artefacts associated with cloning. Using RSCA, a total of six alleles were identified among the 26 cheetahs including four previously found by clonal sequence analysis (ha14-17) and two new alleles (gd01 and gd02). These six alleles were distributed among five phenotypes. This compares with 24 alleles among 20 phenotypes in a similar number of domestic cats confirming the limited DRB variability of the cheetah. RSCA allowed DRB phenotypes to be assigned to individual cheetahs. Fifteen cheetahs were ha14 / ha15 / ha16 / ha17, three were ha15 / ha16 / ha17, six were ha14 / ha16 / ha17, one was ha14 / ha15 / ha16 / ha17 / gd01 and one was ha15 / ha16 / ha17 / gd02. Sequence analysis of gd01 showed it to be a recombinant of ha16 and ha17. The significance of this apparent lack of DRB variability on the cheetah is discussed in the context of cheetah population structures in the wild.

29.13P

FACTORS EFFECTING LEVELS OF MHC CLASS IIB DIVERSITY IN SEA TROUT *SALMO TRUTTA*

[1]Stuart B. Piertney, [2]Philip J. Bacon, [3]Alan Youngson

[1]School of Biological Sciences, University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, UK

[2]Centre for Ecology & Hydrology, Banchory Research Station, Hill of Brathens, Banchory AB31 4BW, UK

[3] FRS Freshwater Laboratory, Faskally, Pitlochry, Perthshire PH16 5LB, UK

It is widely acknowledged that balancing selection acts to retain the remarkably high levels of diversity that are characteristic of MHC genes. However, it remains unclear whether such selection is mediated through antagonistic host-parasite co-evolution or some form of sexual selection. Here we examine the relative contributions of these two processes in natural populations of sea trout. The effects of parasite derived selection is examined by comparison of the levels of MHC class II B diversity, and the patterns of synonymous and non-synonymous amino acid substitution in two trout populations with contrasting levels of parasitism. The potential that disassortative mating between MHC types can be acting to maintain diversity is examined by determining if the frequency of MHC dissimilar pairs among 117 natural matings are greater than would be expected by chance.

29.14P

DOES DRIFT OR SELECTION DEFINE MHC DIVERSITY IN ISOLATED POPULATIONS OF WATER VOLE *ARVICOLA TERRESTRIS*?

[1]Stuart B. Piertney, [2]Sandra Telfer, [1]Xavier Lambin

[1]School of Biological Sciences, University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, UK

[2]Centre for Comparative Infectious Diseases, University of Liverpool, Chester High Street, Neston, Cheshire CH64 7TE, UK

Despite evidence of the adaptive value of MHC diversity, many natural populations display limited MHC polymorphism yet remain viable. It is suggested that such patterns reflect either parasite-driven selection maintaining specific variants, or random genetic drift defining the level and types of diversity that are present. Both processes will affect, to different degrees, individual- and population-level fitness when novel pathogens or new selection pressures arise. Few studies have examined the relative contributions of parasite-driven selection and drift in natural populations, partly because of a lack of appropriate model systems where MHC variation can be determined among isolated populations exposed to different selection regimes through local variation in the prevalence and types of parasites and pathogen. Here we examine the relationship between levels of microsatellite DNA polymorphism, MHC variation, and parasite diversity and prevalence among water vole populations occupying islands off the west coast of Scotland. There is a large range in population size among the islands, together with considerable inter- and intra island variation in parasite load. The microsatellite data thus allows us to examine the contribution of population bottlenecks to overall diversity and hence whether selection regimes are acting to retain or further minimise diversity at the MHC.

29.15P

MHC AND THE OLFACTORY SYSTEM – A CUE FOR SEXUAL SELECTION IN FLYCATCHERS?

Nina Svedin

Dept. of Animal Ecology, Evolutionary Biology Center, Uppsala University, Norbyv. 18 D, S-752 36 Uppsala Sweden

Extensive genetic homozygosity in the Major Histocompatibility Complex (MHC) leads to a badly functioning immune system. It is therefore costly to mate with an individual with similar MHC and selection should favor the evolution of mechanisms for detecting a potential partner's MHC compatibility. Because of the highly polymorphic nature of the MHC, and its influence on specific individual odours, the gene complex might provide a marker for relatedness. If so, MHC disassortative mating preferences may also be a mechanism to avoid mating with close kin. Thus, optimal mate choice based on genetic compatibility in the MHC and also reducing inbreeding depression would be favored by both sexual and natural selection. In humans, mice and fishes it has been shown that females can base their mate choice on olfactory cues. This has however, not before been investigated in birds.

Symposium 30

Evolution of host defences against parasites

Organisers: Arjen Biere & Jacqui A Shykoff

Conference Auditorium 1

09.50 – 10.20	**Mitchell-Olds, T. H.** Molecular and phenotypic variation for insect resistance in *Arabidopsis thaliana* and *A. lyrata.*
10.20 – 11.00	**Coffee**
11.00 – 11.30	**Rausher, M. D.** Experimental analysis of selection in plant-enemy systems.
11.30 – 12.00	**Kraaijeveld, A. R.** Multiple selection pressures on host resistance.
12.00 – 12.20	**Heidel, A. J.** Interactions between herbivore and pathogen resistance in *Nicotiana attenuata.*
12.20 – 12.40	**Restif, O.** Concurrent evolution of resistance and tolerance against pathogens.
12.40 – 14.00	**Lunch**
14.00 – 14.20	**Ågren, J.** Negative correlation between resistance and tolerance to herbivory in the perennial herb *Lythrum salicaria.*
14.20 – 14.40	**Biere, A.** Cost of chemical defense: are trade-offs with growth enhanced under competition?
14.40 – 15.00	**Wegner, K. M.** Constraints in defence gene diversity – the case of sticklebacks and their parasites.
15.00 – 15. 20	**Decaestecker, E.** Constraints in defences of *Daphnia magna* populations.
15.20 – 16.00	**Tea**
16.00 – 16.20	**Van der Veen, I. T.** State dependent trade-off between predation and infection risk mediated via carotenoids.
16.20 – 16.40	**Montserrat, M.** Who is forcing on my door? Flexible anti-predator behaviour in spider mites.
16.40 – 17. 00	**Mallon, E. B.** Specific vs. non-specific immune defence in the bumble bee, *Bombus terrestris* L.
17.00 – 17.20	**Ferrari, J.** Resistance to natural enemies and host plant specialisation in the pea aphid.

Invited talks

30.1

MOLECULAR AND PHENOTYPIC VARIATION FOR INSECT RESISTANCE IN *ARABIDOPSIS THALIANA* AND *A. LYRATA*

Thomas Mitchell-Olds, Juergen Kroymann, Maria Clauss

Max Planck Institute of Chemical Ecology; Beutenberg Campus; Winzerlaer Strasse 10; 07745 Jena, Germany

What evolutionary factors influence insect resistance in natural plant populations? We identified the MAM2 gene, an enzyme-encoding locus responsible for biosynthesis of glucosinolates, biologically active secondary compounds which provide defense against generalist insect herbivores. Fine mapping reveals that MAM2 constitutes an insect resistance QTL, caused by variation in glucosinolate profiles conferred by allelic polymorphism at this locus. A sequence survey of randomly chosen accessions indicates that the MAM2 locus is highly variable among *A. thaliana* ecotypes. Furthermore, statistical methods of molecular population genetics suggest that MAM2 is subject to balancing selection. This may be caused by ecological trade-offs, i.e., by contrasting physiological effects of glucosinolates on generalist vs. specialist insects. We then examined a large, undisturbed population of perennial *Arabidopsis lyrata ssp. petraea.* Data from microsatellites and single copy nuclear loci show high levels of molecular variation compatible with equilibrium neutral models. Quantitative genetic variation for morphological and phenological traits also shows very high levels of genetic variance. However, despite large sample sizes, no heritable variation for resistance to insect herbivores (*Plutella* and *Pieris*) was detectable. This finding contrasts with studies of introduced, weedy, annual plant species. This difference may result from nonequilibrium conditions and population admixture in introduced annual weeds.

30.2

EXPERIMENTAL ANALYSIS OF SELECTION IN PLANT-ENEMY SYSTEMS

Mark D. Rausher

Department of Biology, Duke University, Box 90338, Durham, NC 27708-0338, USA

Experimental analysis of selection in plant-enemy systems has revealed a number of properties of the evolution of species interactions. In particular, recent experiments in a variety of systems indicate that coevolution is likely to be diffuse rather than pairwise. In addition, recent analyses suggest that quantitative allocation to resistance by plants is often not at evolutionary equilibrium, probably due to temporal and spatial fluctuation in the magnitudes of costs and benefits of resistance. Finally, recently obtained evidence suggests that competition among enemies may affect the trajectory of coevolution.

30.3

MULTIPLE SELECTION PRESSURES ON HOST RESISTANCE

A. R. Kraaijeveld

NERC Centre for Population Biology, Imperial College London, Silwood Park Campus, Ascot, Berks. SL5 7PY UK

In a host-parasite interaction, there will be a strong selection pressure on the host to defend itself against parasitism. *Drosophila melanogaster*, several species of hymenopteran parasitoids and a fungal parasite are used as a model system to explore the various types of selection pressure acting on host resistance. Two issues are addressed in detail: 1) Is there a trade-off between host resistance and other fitness parameters? If so, how does such a cost influence the evolution of resistance? Is this trade-off symmetrical? The results show first of all, that resistance is indeed costly in this system, but that the magnitude of the costs are density-dependent. Costs have an effect on the rate of evolution of resistance, but the situation is more complicated than a simple trade-off between two traits. 2) Given that *Drosophila* are attacked by a variety of parasitoids and parasites, how does the evolution of resistance against one natural enemy affect resistance against others? Is there substantial cross-resistance or are there trade-offs? Using an artificial selection approach, it appears that there is a limited amount of cross-resistance, but trade-offs are not found.

Contributed talks

30.4

INTERACTIONS BETWEEN HERBIVORE AND PATHOGEN RESISTANCE IN *NICOTIANA ATTENUATA*

Andrew J. Heidel, Ian T. Baldwin

Max Planck Institute for Chemical Ecology, Winzerlaer Strasse 10, Beutenberg Campus, D-07745 Jena, Germany

Pathogen and herbivore resistance signalling interact synergistically and antagonistically. Studies have shown that pathogen resistance mediated by salicylic acid can inactivate herbivore resistance mediated by jasmonic acid. Conversely, jasmonic acid can also inactivate salicylic acid mediated resistance. However in some cases, jasmonic acid signalling can enhance salicylic acid signalling. Determining the totality of the interaction between jasmonic and salicylic acid with an assay for one chemical or resistance against one organism is difficult due to the complexity the resistance mechanisms mediated by salicylic and jasmonic acid. To better assess the multiple effects of the signalling interaction, we have taken a microarray based approach to determine how induced herbivore resistance affects pathogen resistance using the well characterized *Nicotiana attenuata*/*Manduca sexta* plant/herbivore system. With this system we can detect a wide spectrum of effects from induced herbivore resistance including the pathogen resistance mechanisms themselves and the signalling leading to pathogen resistance.

30.5

CONCURRENT EVOLUTION OF RESISTANCE AND TOLERANCE AGAINST PATHOGENS

Olivier Restif, Jacob C. Koella

Université Pierre et Marie Curie, Parasitologie Evolutive, 7 quai Saint Bernard, CC 237, 75252 Paris Cedex 05, France

Recent experiments on plant defenses against pathogens or herbivores have shown various patterns of association between two strategies: resistance, which reduces the probability of being infected or attacked, and tolerance, which reduces the loss of fitness caused by the infection or attack. We present a host-pathogen model that considers the evolution of resistance and tolerance as two independent traits. Three of the main results are as follows. First, if fecundity decreases linearly as the level of defense increases, tolerance and resistance are mutually exclusive strategies. Conversely if the cost of resistance is more than linear and if mixing resistance and tolerance costs less than investing in pure strategies, our model predicts the evolution of mixed strategies. Second, details of the host-interaction determine the outcome of evolution. For example, if the cost is linear, tolerance against parasites that increase their host's mortality will evolve to higher levels than tolerance against parasites that decrease fecundity. Third, differences in environmental and epidemiological conditions can lead to contrasted outcomes of evolution. One the one hand, conditions that enhance the host's or the parasite's fitness select for high investment in one strategy of defense and lead to a negative correlation between resistance and tolerance (although the model does not assume a trade-off between the two traits). One the other hand, under conditions that enable only little host reproduction or parasite transmission, low investment in both resistance and tolerance evolves and they are positively correlated. In addition, although tolerance and resistance are assumed to be costly (and thus reduce fecundity), variation in environmental conditions can lead to a positive correlation between fecundity and defense among populations. These results emphasize the problems of estimating trade-offs across natural populations.

30.6

NEGATIVE CORRELATION BETWEEN RESISTANCE AND TOLERANCE TO HERBIVORY IN THE PERENNIAL HERB *LYTHRUM SALICARIA*

[1]**Jon Ågren,** [2]Julio Alcantara

[1]*Dept. of Plant Ecology, Evolutionary Biology Centre, Uppsala University, Villavägen 14, SE-752 36 Uppsala, Sweden*

[2]*Dpto. de Biología Animal, Biología Vegetal y Ecología, Universidad de Jaén, Jaén E-23071, Spain*

Resistance and tolerance represent two alternative means for plants to cope with herbivory, and theory suggests that variation in tolerance may contribute to the maintenance of variation in resistance among and within populations. In a field experiment, we quantified variation in resistance and tolerance to insect herbivory among natural populations of the perennial herb *Lythrum salicaria* sampled along a latitudinal transect across Sweden. In addition, we tested the hypothesis that resistance and tolerance are associated with a cost. Resistance and tolerance varied considerably among populations and were negatively correlated. The early-developing northern populations were more tolerant, but less resistant to herbivore damage than the late-developing southern populations. Moreover, tolerance was associated with a cost in terms of low relative growth in the absence of herbivores. Differentiation in phenology of growth can partly explain variation both in tolerance and resistance to herbivores, and this should contribute to the negative correlation observed between the two traits. The results suggest that a full understanding of the evolutionary consequences of plant-herbivore interactions requires that variation in resistance and tolerance are considered jointly.

30.7

COST OF CHEMICAL DEFENSE: ARE TRADE-OFFS WITH GROWTH ENHANCED UNDER COMPETITION?

Arjen Biere, Hamida B. Marak

Dept. of Plant Population Biology, Netherlands Institute of Ecology, NIOO-KNAW, P. O. Box 40, NL-6666ZG Heteren, The Netherlands

Natural plant populations often show genetic variation in levels of chemical defense compounds. Fitness costs of defense are often invoked to explain the maintenance of such variation, but the magnitude of fitness costs is thought to vary with environmental conditions, i.c. increase with increasing environmental stress. We investigated (1) whether there are fitness costs associated with the production of iridoid glycosides (IGs), terpenoid compounds that strongly deter generalist insect herbivores, in ribwort plantain (*Plantago lanceolata* L.), using lines that had been artificially selected for high and low leaf IG concentrations for four generations; (2) whether such costs increase under nutrient and competition stress. Plants selected for high IG levels overall produced fewer inflorescences and had a significantly lower reproductive dry weight than plants selected for low IG levels, indicating a fitness cost of IG production. However, there was no evidence that fitness costs increased with environmental stress. Two factors may have contributed to the absence of higher costs under environmental stress. First, IGs are carbon-based chemicals. Under nutrient limitation, the relative carbon excess may result in the production of IGs without imposing a further constraint on growth and reproduction. Second, there is a positive genetic association between IG level and cotyledon size. In the presence of competitors at low nutrient supply, the negative direct effect of a high IG level on growth is partly offset by a positive indirect effect of the associated larger cotyledon size. Trade-offs between defence and growth therefore appear to be diminished rather than enhanced under competition.

30.8

CONSTRAINTS IN DEFENCE GENE DIVERSITY – THE CASE OF STICKLEBACKS AND THEIR PARASITES

K. Mathias Wegner, M. Kalbe, T. B. H. Reusch, J. Kurtz, M. Milinski

Max-Planck-Institute of Limnology, August-Thienemann-Str. 2, 24306 Ploen, Germany

Recognition of pathogens is crucial for the evolution of host defence against infection. In the vertebrate immune system the striking polymorphism of some Major Histocompatibility Complex (MHC) genes is tightly linked to the capability of pathogen recognition. Therefore polymorphism is attributed to pathogen driven balancing selection, either through overdominance or frequency dependant selection. Previous experiments have shown that mice heterozygous at MHC loci are more resistant to simultaneous infection with two bacterial strains, suggesting a role of heterozygote advantage for maintaining MHC polymorphism. However, theory predicts an optimal intermediate allelic diversity opposed to maximal heterozygosity. Maximal heterozygosity may constrain effective immune responses due to negative selection on T-cell repertoire size or increased autoimmunity. Here, we test the prediction of an optimal immunogenetic diversity for parasite resistance in a species with several functional MHC class IIB loci, the three-spined stickleback *Gasterosteus aculeatus*. We experimentally exposed fish from six lab-bred sibships, each segregating into MHC-genotypes with below optimal, optimal, and superoptimal levels of allelic MHC diversity. To reveal effects of overdominance fish were infected with three different species of parasites (the nematodes: *Anguillicola crassus* and *Camallanus lacustris* and the digenean trematode *Diplostomum spathacaeum*). These parasites represent three of the six most abundant parasites in the host population. Over all sibships we find an optimal diversity of 5.6 MHC class IIB molecules. Within single sibships optimal MHC diversity results in lower parasite transmission rates and thus make the number of MHC alleles a target for natural selection by parasites. The variation in MHC class IIB variants per fish may stem from inter-haplotypic differences in the number of loci or from differences in heterozygosity. Hence, we assessed whether the number of MHC gene duplications can be the target for selection, and measured the relative number of MHC class II loci with quantitative PCR.

30.9

CONSTRAINTS IN DEFENCES OF *DAPHNIA MAGNA* POPULATIONS

[1]**E. Decaestecker**, [1]L. De Meester, [2]D. Ebert

[1]*University of Leuven, Laboratory of Aquatic Ecology, Ch. de Bériotstraat 32, 3000 Leuven, Belgium*

[2]*Université de Fribourg, Unité de Ecologie et Evolution, Chemin du musée 10, CH-1700 Fribourg, Switzerland*

Traditionally, the adaptation and evolution of defences in aquatic ecology have mainly been investigated with respect to predation and competition. Recently, however, it has become apparent that parasites can play a key role in structuring aquatic host populations. Because of the confrontation of host populations with multiple enemies, constraints arose. In this study, we investigate the constraints in defences in *Daphnia magna* populations when confronted with multiple enemies. We explore the interactions between a random set of clones from a *Daphnia magna* population and a set of micro-parasite species co-occurring with the host population and explore how these interactions can shape the evolution of host resistance and parasite infectivity. Further, we broaden the issue of multiple antagonists to different types of antagonists. We investigate how the presence of parasites can constrain predator avoidance behaviour in the *Daphnia magna* host.

30.10

STATE DEPENDENT TRADE-OFF BETWEEN PREDATION AND INFECTION RISK MEDIATED VIA CAROTENOIDS

Ineke T. van der Veen, Lena E. Sivars

Max Planck Institute of Limnology, Dept. of Evolutionary Ecology, August Thienemann Str. 2, D 24306 Plön, Germany

Carotenoids are shown to play an important role in the immune response of animals because of their function as free radical scavengers. *Macrocyclops albidus* copepods store carotenoids for short-term use. Although storing these carotenoids seems advantageous in terms of immune response, the carotenoids, because of their bright orange colour, also cause the copepods to become very conspicuous. Therefore we hypothesise a trade-off between predation risk and infection risk; i.e. in order to avoid predators, copepods need to minimise their carotenoid stores, but in order to avoid infectious diseases copepods need to maximise their carotenoid stores. In a previous study was shown that copepods indeed decreased their carotenoid stores upon increased predation risk and those individuals that decreased their carotenoid storage suffered a higher infection rate with the cestode *Schistocephalus solidus* than the others. Although this result seems very promising, it could be that the high infection rate is not due to the proposed trade-off but due to a correlated response instead. Weak animals may suffer higher predation risk when under threat of predation and therefore they may have to change their carotenoid reserves more than strong individuals. At the same time, weak individuals may have a less well functioning immune system and may become more often infected than strong individuals. In the present study we test for such a potential correlated response by manipulating phenotypic quality, i.e. by comparing sibs that grew up under rich and poor food conditions. We test the response of the sibs from different food conditions to predation risk in terms of carotenoid reserves and we compare subsequent experimental infection rates with *Schistocephalus solidus*.

30.11

WHO IS FORCING ON MY DOOR? FLEXIBLE ANTI-PREDATOR BEHAVIOUR IN SPIDER MITES

Marta Montserrat, Arne Janssen, Sara Magalhaes, Maurice W. Sabelis

University of Amsterdam, Kruislaan 320, 1098 SM, Amsterdam, The Netherlands

Many prey species use spatial or temporal refuges to reduce their predation risk. Refuge use, however, usually entails a cost in terms of reduction in prey energy intake or mating opportunities. Moreover, within each habitat, predation risk is not constant and can vary even within short time periods. An example of predation risk being not constant is when prey is confronted with natural enemies that differ in the risk that they pose. Prey should then respond specifically to each predator species by using refuges from predation in a flexible way, to maximize their reproductive success. We study the anti-predator behaviour of females of an herbivorous spider mite species that build their own refuge in the areas they forage, at expenses of food quality. Thus, refuge areas are expected to be safer from predation but less profitable in terms of food quality. We estimate the future reproductive success of females of this species inside and outside the refuge when exposed to two predator species that differ in the risk that they pose: a specialist predator that can easily overcome the refuge, and a generalist predator against which the refuge is effective. Based on these results, we predict whether females should move from or stay in sheltered areas depending on the predation risk they are exposed to. Subsequently, we test whether spider mite females behave according to the predictions.

30.12

SPECIFIC VS. NON-SPECIFIC IMMUNE DEFENCE IN THE BUMBLE BEE, *BOMBUS TERRESTRIS* L.

Eamonn B. Mallon, Paul Schmid-Hempel

ETH Zürich, ETH Zentrum NW, Zürich, Switzerland

Hosts vary in both their strength of response to a general immunological insult and in their specific susceptibility to different parasite species or different strains of the same parasite. The variation in the general immune response is thought to be due to the costs imposed by selection on defended individuals. The variation in the specific response may originate from variation in host and parasite genotypes and is a requirement for frequency dependent selection. The relationship between these two fundamental aspects of defence has only rarely been studied. Using the bumblebee *Bombus terrestris* and its gut trypanosomal parasite *Crithidia bombi* we found that the host's specific response profile towards different strains correlates negatively with its level of response to a general insult. This is the opposite result, one would expect if the level of general response were simply a measure of immunological quality ("immuno-competence"). Rather it suggests that there is some form of a trade-off between these two fundamental aspects of the immune system. These results, therefore, shed an important light on the possible constraints that affect the evolution of the immune system and particularly the trade off between different arms of the immune system.

30.13

RESISTANCE TO NATURAL ENEMIES AND HOST PLANT SPECIALISATION IN THE PEA APHID

Julia Ferrari, H. Charles J. Godfray

NERC Centre for Population Biology, Imperial College London, Silwood Park Campus, Ascot, SL5 7PY, UK

Our goal is to understand how selection pressures from both lower and higher trophic levels act together to influence host plant use and resistance to natural enemies. The evolution of resistance and host plant specialisation will be influenced by ecological circumstances and the genetic architecture of the traits involved. For example, different plants are likely to attract different natural enemies, so selection for resistance could vary between plant species. Moreover, there might be genetic correlations between plant use and resistance, imposing further constraints on the evolution of resistance. Populations of the pea aphids, *Acyrthosiphon pisum*, vary in their degree of specialisation on different plants and are therefore a valuable model system to address such issues. We will present data on the ability to use five different host plants in a European population of the pea aphid. These will be linked to the aphids' resistance to four of their natural enemies, two parasitoid wasps *Aphidius ervi* and *A. eadyi*, and two fungal entomopathogens *Erynia neoaphidis* and *Zoophthora phalloides*.

Posters

30.14P

RESISTANCE AND TOLERANCE OF *URTICA DIOICA* TO A PARASITIC PLANT: CORRELATIONS WITH CANDIDATE TRAITS

[1]Riitta Ahonen, [2]Tanja Koskela, [3]Susanna Puustinen, [2]Veikko Salonen, [1]Pia Mutikainen

[1]*University of Oulu, Department of Biology, P.O. Box 3000, FIN-90014 University of Oulu, Finland*

[2]*University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FIN-40351 University of Jyväskylä, Finland*

[3]*University of Joensuu, Department of Biology, P.O. Box 111, FIN-80101 Joensuu, Finland*

We studied the basis of parasite tolerance and resistance of the stinging nettle (*Urtica dioica*) against the greater dodder (*Cuscuta europaea*). In a greenhouse experiment we first tested for genetic variation in several life-history, physiological, and morphological traits that potentially contribute to resistance and tolerance to parasitic plants (e.g. root:shoot ratio, relative growth rate, net photosynthetic rate, timing of flowering, nutrient content of the shoot, and vegetative reproduction). Furthermore, we tested whether these traits correlate with previously estimated tolerance and resistance estimates of 19 *U. dioica* families. The traits measured varied among families, which suggests genetic variation and evolutionary potential of these traits. Stem height and relative growth rate in the beginning of the growing season correlated positively with resistance whereas growth at the end of the growing season, net photosynthetic rate, phosphorus concentration, and vegetative reproduction correlated negatively with resistance. These results thus suggest that particular traits rendered some families less suitable as hosts for the parasitic plants. However, none of the measured traits correlated with tolerance, which suggests that variation in the measured traits does not confer to variation in tolerance. This lack of correlations may also indicate that tolerance might be achieved through phenotypic responses induced by the infection, instead of through particular inherent traits of the families.

30.15P

THE EVOLUTIONARY DYNAMICS OF DIFFERENT MECHANISMS OF COSTLY PARASITE RESISTANCE

[1]M. Boots, [2]R. G. Bowers

[1]*University of Stirling*

[2]*University of Liverpool*

Parasite resistant hosts may avoid becoming infected, recover more quickly after infection, remain immune for a long period once they recover or survive longer once infected. We might expect the possession of any of these resistance mechanisms to be costly. A series of models are constructed to examine the evolution of costly host resistance to directly transmitted micro-parasites that examine these distinct mechanisms of avoidance, recovery, immunity and tolerance resistance mechanisms. In each case polymorphism is more likely between very dissimilar strains. However, the region where polymorphism occurs is relatively much smaller when resistance is through reduced pathogenicity or increased immunity. In particular, polymorphism with highly resistant strains requires correspondingly high costs. This is in contrast to avoidance or recovery resistance, where polymorphism can also occur when high resistance is associated with small costs due to the inability of highly resistant strains with low susceptibility or high recovery to support the parasite alone and hence resist invasion by the susceptible strain. We use a combination of two-way invasion plots and pair-wise invasion plots and relate the two approaches, showing that the evolutionary outcome depends crucially on the shape of the constraint function between resistance and its assumed cost in terms of intrinsic growth rates.

3016P

EFFECTS OF *TRYPANOSOMA CRUZI* INFECTION ON THE DEVELOPMENT AND FEEDING BEHAVIOUR OF *MEPRAIA SPINOLAI* (HEMIPTERA; REDUVIIDAE): TESTING THE MANIPULATIVE HYPOTHESIS

C. Botto-Mahan, P. Cattan, R. Medel

Universidad de Chile, Departamento de Ecologia, Las Palmeras 3425, Casilla 653, Santiago, Chile

Parasites have been hypothesized to manipulate the feeding behaviour of their invertebrate vectors so as to increase the probability of transmission to definitive hosts. Partial support for this hypothesis comes from parasite species with salivary transmission. We present laboratory evidence that infection of the kissingbug *Mepraia spinolai* (Reduviidae) with the dejection-transmitted protozoan *Trypanosoma cruzi* delay insect development and increase their biting attempts towards a mouse host. The time taken between the last meal and dejection was reduced in the presence of the parasite, suggesting that parasite-mediated changes in the feeding behaviour of the vector *Mepraia spinolai* may promote the spread of trypanosomes toward definitive hosts.

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30.17P

HOST ALTERNATIONS DECELERATE THE RED QUEEN IN A SOCIAL PARASITE SYSTEM

Miriam Brandt, Susanne Foitzik

Department Biology I, University of Regensburg, Universitätsstr. 31, 93040 Regensburg, Germany

Parasite populations that are confronted with an array of potential host species have several co-evolutionary options. One possible strategy is to specialise on a single host, but shift to new host species if the current hosts evolve counter-adaptations. If less frequently attacked hosts lower their defences, the speed of the arms race between parasite and hosts can be reduced. Here, we compare two populations of the obligate social parasite *Protomognathus americanus*. Both populations of this North American slavemaking ant co-occur with two sympatric host species. At a location in upstate New York, one of the host species is present at frequencies too low to maintain the parasite, whereas at a site in Ohio, both hosts constitute an exploitable resource. At the former site, the slavemaker did not show a preference for either host, whereas at the latter location, the rarer host species was more strongly exploited. In laboratory behavioural experiments, the two host species from New York did not differ in defensive ability against the parasite. In the Ohio community, in contrast, in raids against the rarer host species, host colonies suffered more severely and the slavemaker was more successful. The finding that the host species with the weaker defences is more frequently exploited by the parasite in the field is consistent with the hypothesis of an on-going host switch at the Ohio site. Moreover, we show that hosts and parasites from New York are more effective at raiding and defending than their counterparts from Ohio. The weaker reciprocal adaptations in the Ohio community indicate that the inclusion of a third player into the interaction decelerates the arms race between parasite and hosts.

30.18P

GENETIC VARIATION WITHIN AND BETWEEN NATURAL POPULATIONS OF THE FRESHWATER DIATOM *ASTERIONELLA FORMOSA* IN RELATION TO FUNGAL PARASITISM BY *ZYGORHIZIDIUM PLANKTONICUM*

A. de Bruin, B. W. Ibelings, E. van Donk

[1]*Netherlands Institute of Ecology (NIOO-KNAW), Rijksstraatweg 6, Nieuwersluis, The Netherlands*

[2]*Centre for Limnology, P.O. Box 1299, 3600 BG Maarssen, The Netherlands*

The understanding of the genetic basis for susceptibility and resistance in terrestrial host-parasite interactions has increased over the past decades with the development of various molecular techniques. This knowledge is still lacking in most aquatic host-parasite systems, for instance in phytoplankton and their fungal parasites. Fungal parasites can have significant effects on phytoplankton populations, mainly due to their ability to reduce algal host populations considerably during epidemics, and their host species specificity. AFLP analysis was used to study levels of genetic variation within and between populations of the predominant asexually reproducing freshwater diatom *Asterionella formosa* in relation fungal parasitism by local and foreign isolates of the facultative sexually reproducing fungal parasite *Zygorhizidium planktonicum*. In our two primarily studied *A. formosa* host populations we found high levels of genetic variation both within and between populations, with a higher amount of genetic variation within than between populations. Genetic markers for susceptibility or resistance to fungal parasites were not detected. Infection experiments using a large number of *A. formosa* host strains and *Z. planktonicum* parasite strains revealed different numbers of susceptible and resistant *A. formosa* strains between populations. Virulence levels of local parasite strains tended to be higher on the local host population than on a foreign host population.

30.19P

MICROSPORIDIA MEDIATED SUPPRESSION OF INSECT HOST IMMUNITY

Robert D. J. Butcher

NERC Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berkshire, UK

Infection of the lepidopteran species *Spodoptera litura* or *Plutella xylostella* in peninsular Malaysia with microsporidia (*Vairimorpha necatrix*, *V. imperfecta*, *Nosema xylostella* sp. n. or *N. whitei*) results in a parasite-load-dependent increased susceptibility to lethal infection by entomopathogenic fungi (*Zoopthora radicans*, *Metarhizium anisopliae*, *Nomuraea rileyi* and *Beuvaria bassiana*) and several endoparasitoid species, including the novel (new host record) *Cotesia plutella* upon *Spodoptera litura*. The generality of increased susceptibility to endoparasitoids and entomopathogenic fungi together may suggest a non-specific or general mechanism of reduced insect immunity, although in all four microsporidia species tested the parasite load in the host fat tissue provided the best correlate to the reduced host immunity. However, the ability of apparently novel endoparasitoids to complete development in microsporidia infected host larvae, but not in host larvae with low or no microsporidia infections suggests the presence of a successful specific host immunity against these novel parasitoids rather than a physiological incompatibility of the host for successful parasitoid larvae development. The novel host-parasitoid association (*S. litura-C. plutella*) enabled by microsporidia infection appears restricted in location where it accounts for less than 5% of the total observed parasitism in the field at the transition from wet to dry season when microsporidia epizootics are maximal. What prevents this association gaining in frequency, especially given that parasitoids can act as vectors for the transfer of infective microsporidia spores, is not clear. Preliminary data suggests microsporidosis (microsporidia induced mortality) of both the host *S. litura* and the infected *C. plutella* parasitoid larvae within the host are likely. Whatever the cause, the failure of this microsporidia-parasitoid association to drive through the host population may account for the lack of apparent evolution of host immunity to the parasitoid, but raises the question if other symbiont-parasitoid combinations have played a role in shaping geographical or temporally heterogeneic host-parasitoid immunity co-evolution.

30.20P

BEHAVIOURAL PLASTICITY OR COEVOLUTION? ADAPTIVE SHIFT OF THE ACCEPTANCE/REJECTION THRESHOLD IN THE HOST OF A SOCIAL PARASITE

Patrizia d'Ettorre, Elisabeth Brunner, Juergen Heinze

University of Regensburg, Universitaetsstrasse 31, 97040 Regensburg, Germany

Behavioural flexibility of social responses, such as aggression, has rarely been investigated in solitary and social insects. The acceptance threshold model predicts that a recognition system should not be fixed, but context-dependent (Reeve, 1989). This study tests the acceptance threshold model in a host-social parasite system: the slave-making ant *Polyergus rufescens* and one of its host species, *Formica rufibarbis*.Two host populations - one where the parasite is present and one where it is absent – were compared in their level of aggression against the parasite and alien conspecifics. According to the model, we predicted the possibility of a seasonal change in the acceptance/rejection level of the host species (expressed as aggression-level) linked to the parasite's peak in activity (raiding and colony-founding season). We expected that the aggression-level of free-living *F. rufibarbis* workers from a parasitized population should rise during this period (July and August), whereas the aggression-level of an unparasitized *F. rufibarbis* population should not show substantial changes connected with the parasite's peak in activity. Our results meet this prediction that the parasitized host population becomes more aggressive against the parasite during its raiding season. Being able to detect and possibly kill a *Polyergus* scout searching for host nests can be an effective strategy for a *Formica* colony to prevent slave-raids. Is this adaptation due to a coevolutionary arm-race or to a behavioural flexibility of the host?

30.21P

THE GENETIC BASIS FOR LOCAL ADAPTATION IN A SOCIAL PARASITE SYSTEM

Birgit Fischer, Susanne Foitzik

University of Regensburg, LS Biologie I, 93040 Regensburg, Germany

Parasitism, life at the expense of others, is a common phenomenon in many animal taxa, from simple Plathelminths to vertebrates such as fish and birds. Social parasite systems differ from most parasites because host and parasite are, following Emery's rule, often closely related species (Emery, 1909). In this study we aim to investigate patterns of behavioural virulence and defence for the small European slavemaking ant *Harpagoxenus sublaevis* and its main host species *Leptothorax acervorum*. We further study whether host and parasite populations act as independent evolutionary units by analysing the geographical genetic structure. Colonies of the slavemaker and its host were collected in three geographically distant populations in Germany, Russia and Italy. An additional unparasitized host population was sampled in England. In behavioural studies on the raiding behaviour we found strong interaction effects indicating very localised coevolution and co-adaptation of parasite and host populations. Furthermore, the currently unparasitized English population were most effective in nest defence against the social parasite. For genetical analysis we amplified a 1440-bp fragment of the mtDNA that combines part of the cytochrome oxidase I and II region and uncovered low variability in the mtDNA for *H. sublaevis* (13 polymorphic sites, 9 haplotypes). We found strong geographic structuring with a FST = 0.66 indicating very low gene-flow between the different slavemaker populations. Especially the Italian population is genetically isolated presumably due to the geographic barrier of the Alps. The strong genetic differentiation could be caused by limitation in dispersal capabilities of slavemaker queens, which are mostly wingless. Genetic analysis of the host species *L. acervorum*, where all reproductives are fully winged, showed higher genetic variation and less geographic structuring than the parasite. We further investigate genetic differentiation of parasite and host populations on the nuclear level.

30.22P

SELECTION FOR TWO VIRULENCE COMPONENTS IN A MOSQUITO - MICROSPORIDIA SYSTEM

[1]Mette H. H. Hansen, [2]Jacob C. Koella

[1]Department of Zoology, University of Aarhus, Building 135, 8000 Aarhus, Denmark

[2]Laboratoire de Parasitologie Evolutive, CC237, CNRS UMR 7103, Université P. & M. Curie, 7 quai Saint Bernard, 75252 Paris, France

Parasite virulence comprises fitness reducing effects on several host life history traits. These same traits are modified by selection acting on infected hosts. Thus, any observed level of virulence represents a 'compromise' between two organisms, being reduced by host tolerance strategies and increased by parasite exploitative strategies. Recent theoretical advances have refined our understanding of coevolutionary trajectories in virulence evolution. In such models, specific host life history traits are assumed to evolve under either host or parasite control. However, in natural systems little is generally known about the potential for evolutionary control of host life history in either host or parasite. To improve this situation, the main challenge lies in identifying traits that contribute to virulence in a given system, and to determine the extent to which such traits represent host or parasite strategies. Selection experiments provide a direct method for investigating evolutionary potential. By selecting *Brachiola algerae* microsporidia for their contribution to virulence components in the mosquito *Anopheles stephensi*, we investigated the genetic basis of virulence in this system, and how virulence correlates with parasite fitness. Two aspects of virulence were incorporated into the selection scheme: Delay of host development, and increased juvenile mortality. We found that both aspects of virulence were associated with increased parasite fitness, and both responded strongly to selection. Furthermore, the two virulence components were correlated: Increased juvenile mortality did not result from an increased instantaneous death rate - as usually assumed in models of virulence evolution - but was an indirect effect of delayed host development. This study underlines the importance of regarding virulence as a complex trait, reaching beyond effects on instantaneous death rates. In particular, life history traits other than mortality should not only be considered as evolving in response to parasite virulence. Rather, they may sometimes express virulent parasite strategies themselves.

30.23P

SEPARATING AVIAN BLOOD PARASITES IN A 2-STEP PCR

Olof Hellgren, Staffan Bensch

Department of Animal ecology, Ecology Bulding-Lund university, Sölvegatan 37, S-22362 Lund, Sweden

Many bird species have been found to host several different lineages of blood parasites (Protista, Haemosporida) and some of these are shared across different host species. This creates a very complex system. For example migratory birds expose themselves to two different sets of parasites and vectors in their summer and winter range. To understand such complex system it is essential to take into account that different lineages, species and families of parasites that can occur in the same bird populations, or in the same bird, and that those parasites may compete or interact with each other. We here present a method that for the first time makes a simultaneous PCR typing of the three most important avian blood parasites (*Haemoproteus, Plasmodium* and *Leucocytozoon*). The method combines the high detection rate of a nested PCR with a separating PCR step for *Plasmodium/Haemoproteus* and *Leucocytozoon* which lead to an easy, fast and accurate method to investigate and separate the parasites in the Protista family by using the same blood sample. We have applied this method on bluethroats (*Luscinia svecica*) collected from the Norwegian and Swedish mountain range to investigate the occurrence of different blood parasites over a geographical range.

30.24P

FITNESS CONSEQUENCES OF HERBIVORY IN A LITTORAL HABITAT: EFFECTS OF PLANT GENOTYPE AND ENVIRONMENTAL VARIATION

Tuija Honkanen, Veijo Jormalainen

Section of Ecology, University of Turku, FIN-20014 Turku, Finland

The relative importance of plant genotype and environmental factors for resistance to herbivory and population regulation of plants is not well known. We investigated the effects of plant genotype and environmental variation (variation in herbivory, growing depth and nutrient availability) on five fitness components (resistance, defence (phlorotannin concentration), number of apical tips, length increment and thallus area) in the brown alga *Fucus vesiculosus*. Herbivory significantly decreased the number of apical tips, length increment and thallus area of *F. vesiculosus*. However, genetic variation in resistance was minimal. Environmental variation had a major effect on the resistance to herbivory. Due to herbivory, the algae in the deep end of the vertical distribution had 80% less apical tips than the algae close to surface. The number of apical tips, length increment and thallus area displayed not only substantial genetic variation, but also large phenotypic plasticity in relation to nutrient and light availability. Allocation to phlorotannins showed substantial genetic variation. Compared to the amount of genetic variation phenotypic plasticity of phlorotannins was low. Phlorotannin concentration was the only fitness trait, which displayed significant genotype-by-environment interactions. We suggest that variation in selection and selective pressures (e.g. light, nutrients, herbivory) with depth and nutrient gradients may be crucially important for maintenance of substantial genetic variation in phlorotannin concentration. In this study top-down and bottom-up control had a stronger effect on the fitness of *F. vesiculosus* than algal genotype. Hence, herbivory and its variation along depth gradient seem to be crucial for the success of *F. vesiculosus* populations, but we found no evidence that herbivory would generate selection among genotypes.

30.25P

FEAR, SEX AND PARASITES: DOES PREDATOR THREAT INDUCE TERMINAL REPRODUCTIVE EFFORT AND IMMUNE SUPPRESSION IN RATS?

[1]Peeter Hõrak, [1]Lea Tummeleht, [2]Heli Talvik

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

[2]*Estonian Agricultural University, Faculty of Veterinary Medicine, Kreutzwaldi 62, Tartu 51014, Estonia*

Increased reproductive effort is proposed to lead to paying survival costs of reproduction due to immunosuppression and resulting susceptibility to pathogens and parasites. However, this hypothesis been difficult to prove in wild animals because the causes of death and infection status of individuals whose reproductive effort was manipulated usually remain unknown. We test this hypothesis in a novel model system consisting of male lab rats, exposed to predator (cat) odour and infected with a neurotropic nematode parasite *Toxocara canis*. We present the results of an experiment testing whether the exposure of rats to predator odour causes increased mating effort (copulation activity) and whether and how this treatment affects the host resistance to experimental infection and other immune parameters.

30.26P

HOW COCCIDIAN PARASITES AFFECT HEALTH AND APPEARANCE OF GREENFINCHES

[1]Peeter Hõrak, [1]Lauri Saks, [1]Ulvi Karu, [1]Indrek Ots, [2]Peter F Surai, [3]Kevin J. McGraw

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

[2]*Avian Science Research Centre, Scottish Agricultural College, Ayr KA6 5HW, UK*

[3]*Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853*

The theory of parasite-mediated sexual selection suggests that coevolutionary arms races between parasites and their hosts are responsible for the evolution of conspicuous ornamental traits used as signals of individual quality in sexual selection. However, still little is known about the mechanisms by which parasites affect the expression of ornamental traits. We manipulated experimentally the levels of an intestinal coccidian parasite, *Isospora lacazei*, in captive male greenfinches (*Carduelis chloris*) and recorded the effect of infection on 14 (mainly hemato-serological) condition indices. Additionally we measured changes in color and carotenoid content of yellow tail and breast feathers, which serve as sexually dimorphic ornamental traits. 89 % of birds hosted chronic isosporan infection before the experiment. Yet experimental inoculation with mixed parasite strains resulted in drastic but transient decreases in serum carotenoid, vitamin E, triglyceride and albumin concentrations and reduced body mass, indicating serious pathology and probable nutrient malabsorption due to damaged intestinal epithelium. Lab-grown tail feathers of infected birds contained 52 % less carotenoids and had also smaller values of chroma and hue than these of the cured birds, indicating the effect of parasites upon the expression of ornamental traits. The strong pathogeneicity of secondary infection suggests high antigenic diversity of different isosporan strains. Hence, our results present the direct experimental support for one of the basic premises of parasite-mediated sexual selection, namely that parasites affect the expression of secondary sexual traits.

30.27P

SUPER-BEE VS. RED QUEEN: HAPLOTYPE FITNESS IN A BUMBLEEBEE HOST SYSTEM

Alice Johnson

ETH Zürich, Ecology and Evolution, ETH Zentrum NW, Clausiusstr. 25, CH-8092 Zürich, Switzerland

Much has been written about the possible importance of cyclical changes in genotype frequency to allow a host to escape from parasitism (the Red Queen effect). We attempted to assess the importance of common and rare genotyopes in a population of the bumblebee, *Bombus terrestris*. Spring queens were divided into common and rare genotypes by looking at the frequency of different haplotypes in the population (from a non-coding area on the mitochondria). Colonies were divided into 3 groups; common haplotype 1, common haplotype 2 and a mixed group of rare haplotypes and were placed in field boxes. The parasite prevalence and fitness over the summer were recorded. Surprisingly, rare haplotypes perform significantly worse than common ones, and there seem to be no differences in parasite prevalence. It seems perhaps intuitive that these haplotypes are rare as they perform less well. It may be that this effect is due to differences in mitochondrial enzyme functioning, creating strong effects upstream from, for example, immune parameters and helping to explain why colony effects are always so great in experimental work

30.28P

RESISTANCE VARIATION IN A SPATIAL CONTEXT OF A HOST-PATHOGEN METAPOPULATION

Anna-Liisa Laine

Department of Ecology and Systematics, PO Box 65, FIN-00014 University of Helsinki, Finland

The coevolutionary arms race between parasites and their hosts results in fluctuations in local population sizes of both counterparts and may constitute a driving force also at the genome level. These dynamics may lead to differentiation among local demes of both hosts and pathogens in their resistance-pathogenicity structures and these differences may become particularly pronounced in situations where local populations are fragmented in space forming metapopulations with varying degrees of interconnectedness between the local demes. Theory predicts these differences to reflect the dispersal scale of both species - for highly mobile species variation among local populations should be less pronounced than for species dispersing over relatively small scales. This study was designed to test whether adjacent potential host populations show marked differences in the identity and frequency of particular host resistance phenotypes, and whether these differences are related to their spatial location and disease status. The study system is located in the Åland Islands, SW-Finland where *Plantago lanceolata* is a host to its powdery mildew, *Podosphaera plantaginis* (Erysiphales), a wind-spread obligate parasite. The pathosystem is characterized by a highly fragmented distribution of the host and aggregated pathogen distribution over the regional scale. Host resistance was studied using a cross-inoculation design of four pathogen strains, obtained from two of the study populations. Altogether eight host populations are studied, each represented by eight individuals. Preliminary results indicate striking differences in the resistance structure both within and among host populations. Although *P. lanceolata* is a wind-pollinated species, its seeds are dispersed over short distances and the species commonly forms side rosettes. These life cycle features coupled with local population disease history are likely to attribute to the observed variation.

30.29P

IMPORTANCE OF MHC GENES AND DIETARY CAROTENOIDS DURING INFECTION IN THE THREE-SPINED STICKLEBACK

[1]Åsa Langefors, [1]Dennis Hasselquist, [2]Joachim Kurz, [2]Martin Kalbe, [2]Manfred Milinski

[1]Lund University, Ecology Building, 223 62 Lund, Sweden

[2]Max Planck Institute for Limnology, Plön, Germany

We have studied the importance of genes versus environment during an infection. We used the MHC (Major Histocompatibility Complex) class II B genotype as genetic factor and dietary carotenoid content as environmental factor in this experiment with the three-spined stickleback *Gasterosteus aculeatus* as model organism. MHC-genes encode cell-surface molecules that are involved in the recognition part of the immune-system. These genes are extremely variable and have been shown to be important for parasite resistance and mate choice in sticklebacks. Carotenoids are important anti-oxidants and play an important role in male ornamentation in sticklebacks. Wild-caught, adult sticklebacks, were mated and full-sib broods were divided into two groups, which were provided with either of two diets; one with high carotenoid level and the other one with low levels of carotenoids. After eight months all fish were infected with the parasite *Schistocephalus solidus*. Two months post-infection, we registered infectious stage and took various condition measures. We took photographs of red males which were later analysed for intensity of the red coloration. All fish have been screened for MHC class IIB genotype. A random subsample from each treatment in each brood was used for studies of immunocompetence and level of oxidative stress.

30.30P

PARASITES PROMOTE CONVERGENCE IN HOST DEFENSIVE TRAITS

R. Medel, M. Mendez

University of Chile, Department of Ecology, Casilla 653, Santiago, Chile

Theory of evolutionary convergence assumes that structurally equivalent phenotypes of ancestrally unrelated species evolve toward similar states by natural selection. The effects of convergence are often seen, but the underlying causes are difficult to disentangle and remain unclear. Three criteria must be satisfied to demonstrate evolutionary convergence. First, the species must be phylogenetically independent, such that convergent traits evolved separately. Second, an adaptive mechanism must be identified and tested to establish that natural selection is the cause of convergence. Third, the traits must be more similar in derived than ancestral species. To our knowledge, these three criteria have never been tested in natural populations. Hence, there is no unequivocal example of convergent evolution. Here we examine the role of parasitism in driving host evolutionary convergence in a host plant-parasitic plant system composed by the mistletoe *Tristerix aphyllus* and the cactus hosts *Echinopsis chilensis* and *Eulychnia acida*. Results from a 5-year field study revealed that spine length, a trait providing defense against the mistletoe, evolve under positive directional selection in the two host species. We mapped spine length onto independent CpDNA phylogenies, and found that spines of *E. chilensis* and *E. acida* were more similar than spines of their unparasitized ancestral species, therefore verifying a crucial element of the hypothesis. These results highlight the importance of host-parasite interactions for broad patterns of convergence, and support the theory that natural selection drives convergent evolution in natural populations.

30.31P

ADAPTIVE INNATE IMMUNITY? RESPONSIVE-MODE PROPHYLAXIS IN THE MEALWORM BEETLE *TENEBRIO MOLITOR*

Y. Moret

University of Sheffield, Department of Animal and Plant Sciences, Western Bank, Sheffield S10 2TN, UK

A primary infection by a parasite may indicate a higher risk of being re-infected in the near future as such enemies become more abundant in the environment. This might have been a contributing factor leading to the selection of acquired immunity in vertebrates. Acquired immunity does not exist in invertebrates despite the fact that they also face increased risks of re-infection following a primary exposure. However, when subjected to immune insult, insects can produce persistent immune responses that may provide prophylaxis. Since these immune responses are costly, persistence must be maintained through a selective advantage. The possibility that such immune responses provided increased resistance to later infections was tested by experimentally mimicking a primary immune insult (pre-challenge) in larvae of the mealworm beetle, *Tenebrio molitor*, with lipopolysaccharides (LPS) prior to early or late exposure with spores of the entomopathogenic fungus *Metarhizium anisopliae*. The results show that pre-challenged larvae produced a long lasting antimicrobial response, which provided either a survival benefit when the larvae were exposed to fungal infection, and a cost when they were not. These observations suggest that the observed response is functionally "adaptive".

30.32P

LOCAL AND REGIONAL PATTERNS IN THE DEFENCE OF *SALIX TRIANDRA* IN NATURAL POPULATIONS AGAINST A RUST

Lena Niemi, Anders Wennström, Lars Ericson

Dept. of Ecology and Environmental Science, Umea University, SE-901 87 Umea, Sweden

Patterns in host defence against pathogens and the virulence of pathogens have rarely been studied in natural populations. The few existing studies have mainly worked on small scales and rarely combined large and small scale studies of the defence and virulence patterns. *Salix triandra* is a widely distributed willow species from Japan to Western Europe. In Sweden it is a rare plant occurring in scattered populations along river valleys. The rust fungus *Melampsora amygdalinae* is host specific to *S. triandra* and is known throughout the distribution range of the host plant. In this study we have focused on the resistance and virulence patterns of the host plant and the rust in natural occurring populations. To study the regional pattern of resistance and virulence, plants were collected from three Swedish host populations and from one host population from the main distribution area in Russia. The rust was collected from the same populations. To study the local pattern of resistance and virulence we collected plants and rust fungi from populations within Swedish river valleys. The result of the inoculation experiments show that the patterns of defence and virulence vary depending on the scale studied. The reason for the adaptation and lack of adaptation of the rust to the different host populations is discussed.

30.33P

FEMALE COLORADO POTATO BEETLES ARE MAKING MATING AND REPRODUCTION DECISIONS ACCORDING TO THE IMMUNE STATUS OF THEIR MATES

[1]Indrek Ots, [1]Dalial Freitak, [2]Alo Vanatoa

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

[2]*Institute of Zoology and Botany, Estonian Agricultural University, Riia 181, Tartu, 51014, Estonia*

The theory of parasite-mediated sexual selection suggests that females should choose their mates according to males' immune status. Indeed, there are number of studies indicating that females prefer to copulate with males expressing superior immunity. Unfortunately, in our knowledge there are no studies describing possible modification of females' mating behavior when female is forced to mate with good or bad quality male. In current study we show that female Colorado Potato Beetles (*Leptinotarsa decemlineata*) modify their mating behavior in respect of mates' immune status. Male total haemocyte count (THC) was significantly higher in the pairs where females attempted to dislodge males during mounting and/or copulation either by brushing against the substrate, by kicking with their hind legs or by pulling their abdomen beneath the elytras. Interestingly, such relationship between dislodging behavior and males' THC was found only in the beetles originated from one of the two studied potato fields. Additionally, mates of the egg-laying females (i.e. females who started to lay eggs within the ten days following copulation) had fewer haemocytes compared to mates of non egg-laying females. The main conclusion of current study is that female Colorado Potato Beetles indeed modify mating behaviour and reproduction decisions according to immune status of their mates. Such decisions might depend on the origin of beetles also.

30.34P

RELATEDNESS AFFECTS COMPETITIVE PERFORMANCE OF A PARASITIC PLANT (*CUSCUTA EUROPAEA*) IN MULTIPLE INFECTIONS

[1]Susanna Puustinen, [2]Tanja Koskela, [3]Pia Mutikainen

[1]*Department of Biology, University of Joensuu, P.O. Box 111, FIN-80101 Joensuu, Finland*

[2]*Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, FIN-40351, Finland*

[3]*Department of Biology, University of Oulu, P.O. Box 3000, FIN-90014 University of Oulu, Finland*

Empirical studies of multiple infections by parasitic organisms are rare even if several theoretical models have shown that parasite relatedness affects the outcome of competition between parasites, and consequently the evolution of parasite virulence. Using a novel study system, namely the holoparasitic plant – host plant interaction, we studied whether parasite relatedness affects competition between parasitic plants (*Cuscuta europaea*) that share common host individuals (*Urtica dioica*). In a greenhouse experiment, we infected host plants with two parasitic plants that were either siblings (single infection) or not related (mixed infection). The average parasite biomass did not differ between single and mixed infections. However, relative size asymmetry (in terms of biomass) between the two competing parasitic plants was significantly higher in the mixed infections compared to the single infections. This result agrees with the predictions of theories of kin-s election and evolution of virulence: through enhanced parasite transmission, selection may favour reduced competition of parasites with genetically related individuals in hosts infected by several parasite genotypes. However, in contrast to the predictions of models on the evolution of parasite virulence, mixed infections were not more virulent than the single-genotype infections. This might be due to the short duration of our experiment.

30.35P

THE BITTERLING-MUSSEL SYMBIOSIS: A MODEL FOR HOST-PARASITE ADAPTATION

[1]Martin Reichard, [2]Carl Smith

[1]Institute of Vertebrate Biology Academy of Sciences of the Czech Republic, Kvetna 8, Brno, Czech Republic

[2]Queen Mary University of London, Mile End Road, London, United Kingdom

Bitterlings (Acheilognatinae) are a monophyletic group of cyprinid fishes that lay their eggs in the gill chamber of freshwater mussels. Female bitterling develop a long ovipositor that insert into the exhalant siphon of a mussel and males fertilise the eggs by releasing sperm over the inhalant siphon of the mussel. Embryos hatch within 2 days but develop inside the mussel for further 3 to 6 weeks. Further, the mussels used for oviposition have larvae that are obligate ectoparasites of fish. I review current knowledge on the status of the bitterling-mussel symbiosis (mutualistic, commensal or parasitic) by summarising the costs and benefits to both symbionts. Second, I show how both symbionts have evolved behavioural, morphological and physiological adaptations, with particular focus on host defence; including mussel rejection of bitterling embryos, differential glochidia load among coexisting fish species and embryo adaptation to the low oxygen environment in the mussel's gill chamber. Finally, I use a recent well-resolved bitterling phylogeny to show the potential of this model system to study the evolution of this symbiosis, which is a part of the ongoing study.

30.36P

EVOLUTION OF A PATHOGEN RESISTANCE PATHWAY IN *LYCOPERSICON PERUVIANUM*

Laura E. Rose, Martin Groth, Gabriele Büttner, Wolfgang Stephan

University of Munich, Luisenstr. 14, 80333 Munich, Germany

We have investigated how a signaling pathway involved in pathogen recognition and defense has evolved in a natural plant population. Two genes are required for resistance to a bacterial pathogen of tomato, *Pseudomonas syringae pv tomato. Pto* has been identified as the receptor for the pathogen ligand, and the closely linked *Prf* is required for activating the resistance response once the pathogen has been detected. Our study focuses on molecular variation in a natural population of *Lycopersicon peruvianum*, a self-incompatible species in the tomato genus, to identify the evolutionary forces acting at these loci. We are evaluating 1) relationships between pathway position and selective constraint 2) epistatic interactions between the two genes, and 3) functional consequences of naturally occurring amino acid variation (using both whole-plant inoculations with the bacterial pathogen and transformation of *Pto* alleles into plants lacking functional copies).

30.37P

DIRECT AND INDIRECT DEFENCE: COMPATIBLE OR CONFLICTING PLANT STRATEGIES?

[1]Joanneke H. Talsma, [2]Jeff A Harvey, [3]Saskya van Nouhuys, [1]Arjen Biere

[1]*Dept. of Plant Population Biology, Netherlands Institute of Ecology, NIOO-KNAW, P.O. Box 40, NL-6666ZG, Heteren, The Netherlands*

[2]*Dept. of Multitrophic Interactions, Netherlands Institute of Ecology, NIOO-KNAW, P.O. Box 40, NL-6666ZG, Heteren, The Netherlands*

[3]*Dept. of Ecology and Systematics, 441 Corson Hall, Cornell University, Ithaca, NY 14853, USA*

Plants in natural populations have to defend themselves against a multitude of natural enemies. They can do so by several mechanisms. Direct defence mechanisms include morphological and chemical factors. Indirect defence mechanisms include the attraction of natural enemies of the herbivores by emitting volatiles or by providing shelter or food. A conflict between these two mechanisms can arise when direct plant defence chemicals are sequestered by herbivores and have harmful effects on their natural enemies (the indirect defence), or if there are trade-offs between the production of direct defence chemicals and (indirect defence) volatiles. We study under which conditions such conflicts arise and the fitness consequences of genotypic variation in direct and indirect defence, using *Plantago lanceolata* and its herbivore-parasitoid complex as a model system. We find that genotypic variation in secondary metabolites in *P. lanceolata* differentially affects the parasitoids of specialist and generalist herbivores and discuss the implications for the evolution of plant defence.

30.38P

HOST CONDITION AND INFECTION SUCCESS OF *TOXOCARA CANIS* LARVAE IN THE LABORATORY RAT

[1]Lea Tummeleht, [2]Heli Talvik, [1]Peeter Hõrak

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

[2]*Department of Parasitology, Estonian Agricultural University, Kreutzwaldi 62, 51014 Tartu, Estonia*

Costs of exploiting organism's immune function are expected to form a basis of many life-history trade-offs. However, despite of extensive research in different model systems used by evolutionary animal ecologists, the evidence about relationships between the status of individuals' immune system (estimated on the basis of various immune parameters) and actual parasite resistance has remained scarce. We address this issue in a novel model system consisting of male lab rats infected with a neurotropic parasite *Toxocara canis*. *T. canis* is a common nematode with the direct life-cycle, infecting canines worldwide. Rodents are paratenic hosts for *T. canis*, which means that parasites use them as vectors but are not interested in keeping hosts alive for a prolonged period. Such parasites are expected to debilitate their hosts seriously and hence one might expect that the infection success of *T. canis* is particularly sensitive to host general condition and immune status. We will present the data about how infection success of *T. canis* in laboratory rats is related to indices of host immune system activation, such as differential leukocyte counts, hormone profiles and organ masses.

30.39P

HORIZONTAL GENE TRANSFER AND GENE DUPLICATION IN POX VIRUSES

Claus Vogl

University of Veterinary Medicine, Veterinaerplatz 1, A-1210 Vienna

Analyses of whole genome data often reveal that some genes have evolutionary histories that diverge from the majority phylogeny estimated for the entire genome. We present a probabilistic model that deals with heterogeneity among gene trees, implement it via the Gibbs sampler, and apply it to a set of chordopox viruses. Pox viruses have the molecular machinery for recombination available, but only co-infection within the same cell will actually lead to substantial gene exchange. Hence, horizontal gene transfer is a possibility but depends on ecological parameters. In our analysis, we find lots of deviation from a common phylogeny among protein loci, but these deviations follow a clear pattern: within the presumably monophyletic groups of capri-lepori-yata-suipoxes (CLYS-group) and the orthopoxes, we find so much evidence of horizontal gene transfer that inference of a phylogeny within these groups is impossible. With respect to evolution, these two groups should therefore be treated as populations. On the other hand, we find very little evidence of deviation from the unrooted phylogeny (Fowlpox, Molluscipox,(CLYS-group,orthopoxes)). For the deviations that we observe, there is strong evidence of gene-duplication/gene-loss, i.e., paralogy. Recombination within closely related groups of chordopox viruses seems therefore important for virus evolution (and therefore of adaptation to the host). But horizontal gene transfer outside of closely related groups seems absent, and therefore does not contribute to viral adaptation.

30.40P

GENOME-WIDE STUDY OF INDUCED IMMUNE RESPONSES AFTER PARASITOIDS ATTACK

[1]Bregje Wertheim, [2]Alex R. Kraaijeveld

[1]University College London/Centre for Evolutionary Genomics, Department of Biology, Darwin Building, Gower Street, London WC1E 6BT, United Kingdom

[2]Imperial College London, Silwood Park Campus/NERC Centre for Population Biology, Ascot, Berkshire SL5 7PY, United Kingdom

Genetic mechanisms for immune responses in insects have mostly been studied for bacterial and fungal challenge. In the ecology of many insects, however, parasitoids pose a formidable threat. The attack by parasitoids is lethal and insects can only survive an attack by launching a rapid immune response. This immune response is different from those for bacteria and fungi. It comprises recognition of non-self, production of specialised blood cells, and encapsulation of the foreign body. The genetics underlying the induced immune response after parasitoid attack are mostly unknown. Using whole genome micro-arrays, we studied gene expressing for an induced immune response in *Drosophila melanogaster* larvae after attack by the parasitoid *Asobara tabida*. Approximately 50 genes showed significantly different behaviour in control and parasitised larvae within the 3 days spanning the immune response. Annotation of these 50 genes reveals that almost 50% is of unknown molecular function and only 10% was previously assigned to an immune or defensive response. Further studies are scheduled to compare genes for the induced responses with genes that changed during evolution for parasitoid resistance.

30.41P

PARASITES LOWER *DAPHNIA* HYBRID FITNESS

Justyna Wolinska, Barbara Keller, Kerstin Bittner, Sandra Lass, Piet Spaak

EAWAG/ETH, Ueberlandstrasse 133, 8600 Duebendorf, Switzerland

In Greifensee (Switzerland), *Daphnia galeata* × *hyalina* hybrids co-occure with both parental taxa. Hybrids are the most abundant taxon suggesting ongoing hybrid superiority. In addition to many known factors which promote hybrids, specific environmental conditions favouring parental species must also exist. We investigated the influence of the gut parasite *Caullerya mesnili* on the *D. galeata* × *hyalina* species complex. Up to 22 % of *Daphnia* were infected by *C. mesnili* in October 2002. Food resources might play an important role in *C. mesnili* prevalence fluctuations. *C. mesnili* dramatically reduced fecundity of its hosts – 2 % of infected individuals carried eggs compared to 70 % in the uninfected group, which suggests a strong selection pressure from *C. mesnili*. Our results indicate that hybrids were the most frequently infected class, whereas parental *D. galeata* were almost resistant. We also found evidence of genetic variation for resistance within taxa; as some hybrid clones were over- or under- parasitized. Resistance of *D. galeata* might counter balance ongoing hybrid superiority and therefore contribute to the maintenance of coexistence of hybrids and parental species in this lake.

30.42P

EFFECTS OF WITHIN- AND BETWEEN-COLONY TRANSMISSION OF *CRITHIDIA BOMBI* ON VIRULENCE IN *BOMBUS* SPP. HOSTS

C. P. Yourth, P. Schmid-Hempel

ETH-Zurich, Ecology & Evolution, ETH-Zentrum NW, CH-8092 Zurich, Switzerland

In the wild, *Bombus* spp. bees may contract infections of the trypanosome parasite *Crithidia bombi* from their nestmates or while foraging on contaminated flowers. Recent studies have shown that recent co-evolutionary association of a microparasite with a host strain can result in higher parasite virulence in that host strain. We expect that as *C. bombi* infections spread within a given colony, the virulence of the infection will increase, while at the same time the virulence in individuals from unrelated colonies will be reduced. To test our prediction we passed cocktails of *C. bombi* strains through workers from a "focus" colony. Seven days after the initial infection of a bee, we collected *C. bombi* from its faeces and used them to infect workers from an unrelated "test" colony as well as additional workers from the "focus" colony. Infections were passaged through workers from 10 reciprocal pairs of colonies (each colony acting as a "focus" and "test"colony) for a total of 20 colonies, with 4-5 serial passages through each. The infected bees were later dissected and the intensities of *C. bombi* infections were scored. The mean infection intensities of the *C. bombi* in the "focus" and "test" colonies were then analyzed using a repeated measures ANOVA. Contrary to our expectation, virulence (measured as infection intensity) did not increase with successive passages in the "focus" colony but decreased significantly in the "test" colonies.

Index to contributors