

FIFTH CONGRESS
of the
EUROPEAN SOCIETY
for
EVOLUTIONARY BIOLOGY



Edinburgh, Scotland

4th-8th September, 1995

Timetable, Abstracts and Delegate List

Boomsma

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of the
EUROPEAN SOCIETY
for
EVOLUTIONARY BIOLOGY

Edinburgh, Scotland
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With assistance from:

University of Edinburgh
City of Edinburgh District Council
Lothian and Edinburgh Enterprise Ltd.
Genetical Society of Great Britain
International Society for Biochemical Systematics
European Science Foundation
Royal Society of London

Thursday 17⁰⁰
poster presentation

Organisers:

Prof. N.H. Barton,
ICAPB, Division of Biological Sciences,
University of Edinburgh
West Mains Road, EH9 3JT
Scotland

P.S.B. Niven
UnivEd Technologies,
Abden House,
1 Marchhall Crescent, EH16 5HP
Scotland

ESEB '95: timetable



	Monday	Tuesday	Wednesday	Thursday	Friday
8.30 Plenary lecture George Square Lecture Theatre	W Scharloo: <i>Evolutionary change - smooth or jumpy?</i> <i>Presidential address</i>	DH Erwin: <i>The end-Permian mass extinction: what difference did it make?</i>	<i>Discussion on applied ev. st. Biol</i>	E Szathmari: <i>Towards a classification of replicators with juicy examples</i>	J Maynard Smith: <i>Animal language and human language</i>
9.30 Appleton Tower	4) The genetic basis of adaptation and speciation LT4 5) The evolutionary biology of trees and forests LT2 11) The evolution of plasticity LT5	2) Processes of molecular evolution LT4 14) Interactions between parasite transmission and host sexual strategy GS 15) Evolutionary radiations and development LT2 6, 9, 11 continued	3) Evolution of plant-parasite interactions LT2 10) Complex dynamics and evolution LT3 17) Hybrid zones LT4 2, 8, 16 continued 2 moves to LT1	1) The Red Queen: selection for genetic diversity LT2 7) Conflicting and concordant data sets in molecular systematics LT4 13) Chromosomal variation and evolution LT1 8, 10, 16 continued	12) Selfish genetic elements LT1 1, 7, 8, 17 continued 17 moves to LT 5
Coffee 11.00 11.30	4, 5, 11 continued	2, 9, 11, 14, 15 continued	3, 8, 10, 16, 17 continued	1, 7, 8, 13, 10, 16 continued	1, 7, 8, 10, 12, 17 continued
Lunch 13.00 Teviot Row	ESEB officers meeting Appleton Tower	ESEB Council meeting Appleton Tower			
14.00 Appleton Tower	6) Developmental stability LT1 9) Evolution of life cycles and mating systems in lower plants and fungi LT3 4, 5, 11 continued	8) Behaviour and evolution GS 16) Current topics in population structure LT5 2, 9, 11, 15 continued 11 moves to LT1	Excursions (Depart 2pm, George Sq) a) Royal Botanic Gardens b) Silurian fossils and palaeoenvironment in the Pentland Hills c) Tour of Glenkinchie Distillery d) Edinburgh Zoo e) Birdwatching in the Forth Estuary	3, 7, 8, 13, 14, 16 continued 14 moves to LT3	7, 8, 10, 12, 17 continued
Tea 15.30 16.00	4, 5, 6, 9, 11 continued	2, 8, 9, 11, 15, 16 continued		3, 7, 8, 13, 14, 16 continued	1, 7, 8, 10 continued International Society of Biochemical Systematics business meeting LT4 17.30
18.00-19.30 Evening meal Pollock Halls					
	<i>Journal of Evolutionary Biology</i> Editorial board 20.00	Civic/University reception 17.45. Playfair Library. Old College	ESEB business meeting South Hall, Pollock Halls 20.30	Banquet: Royal Museum of Scotland	Ceilidh: South Hall, Pollock Halls 20.00

TIMETABLE

1) The Red Queen: selection for genetic diversity	LT2	Thu-Fri
2) Processes of molecular evolution	LT4/1	Tue
3) Evolution of plant-parasite interactions	LT2	Wed-Thu
4) The genetic basis of adaptation and speciation	LT4	Mon
5) The evolutionary biology of trees and forests	LT2	Mon
6) Developmental stability	LT1	Mon-Tue
7) Conflicting and concordant data sets in molecular systematics	LT4	Thu-Fri
8) Behaviour and evolution	GS	Tue-Fri
9) Evolution of life cycles and mating systems in lower plants and fungi	LT3	Mon-Tue
10) Complex dynamics and evolution	LT3	Wed-Fri
11) The evolution of plasticity	LT5	Mon-Tue
12) Selfish genetic elements	LT1	Fri
13) Chromosome variation and evolution	LT1	Thu
14) Interactions between parasite transmission and sexual strategy	GS/LT3	Tue, Thu
15) Evolutionary radiations and development	LT2	Tue
16) Current topics in population structure	LT5	Tue-Thu
17) Hybrid zones	L4/5	Wed, Fri

*In most cases, the first author will present the paper; where this is not the case, the presenter is in **bold**. Abstracts are listed alphabetically by presenter in the following section; the numbers given for each talk/poster are in this order.*

LT1 · Appleton Tower Lecture Theatre 1 etc
GS · George Square Lecture Theatre

1) The Red Queen: selection for genetic diversity

Dieter Ebert, Zoology Dept., Univ. of Oxford, South Parks Road, OX1 3PS, UK

Andrew Read, ICAPB, Univ. of Edinburgh, West Mains Rd., EH9 3JT, UK

Appleton Tower Lecture Theatre 2

Thursday

Chair: A Read

Plants and pathogens

9.30 - 10.00

99a

Ebert D

The co-evolution of virulence

10.00 - 10.30

47

Brown JKM

Genes and memes in the evolution of disease resistance in crops

10.30 - 11.00

174

Kelley S

The Red Queen, a grass and its viruses

Coffee

Chair: A Read

Ancient asexuals

11.30 - 11.50

170

Judson OP

Preserving genes: the maintenance of genetic diversity in a model metapopulation

11.50 - 12.10

197

Little TJ & Hebert PDN

Cryptobiosis, the Red Queen, and the myth of the ancient asexual

12.10 - 12.30

360

Thomas R & Norton RA

Long-term parthenogenesis and the evolution of acariform mites

12.30 - 12.50

419

Kondrashov AS & Yampolsky L

The evolution of recombination under fluctuating selection: when is it possible?

Friday

Chair: D Ebert

Catching the Red Queen

9.30 - 9.50

198

Lively CM, Jokela J & Dybdahl M

Through the looking glass: parasites sex and clonal diversity in a New Zealand snail

9.50 - 10.10

166

Jokela J & Lively CM

Parasites, sex and early reproduction in a mixed population of freshwater snails

10.10 - 10.30

296

Read AF, Morris K, Gemmill A & Viney ME

Is sexual reproduction by parasitic nematodes an immune evasion strategy?

10.40 - 11.00

137

Gulbrandsen B

Variation in mating rate in hermaphrodites maintained by a sexually transmitted disease

Coffee

Chair: J Jokela

11.30 - 11.50

263

Okamura B, Jones CS & Noble LR

Extreme genetic homogeneity in a cyclically clonal freshwater bryozoan

11.50 - 12.10

388

Vernon JG, Okamura B & Noble LR

Temporal patterns in the genetic structure of a parasitised population of freshwater bryozoans

12.10 - 12.30

404

Weinzierl RP, Schmidt P, Berthold K, Beukeboom LW & Michiels NK

The cost of sex for a hermaphrodite: how much does the flatworm *Dugesia polychroa* (Turbellaria, Platyhelminthes) pay?

12.30 - 12.50

239

Mokievsky VO

A new modification of the Red Queen hypothesis: wild-geese chase in anthropogenic transformed ecosystems

Friday

Chair: D Ebert

16.00 - 16.20

403

Wedekind C, Seebeck T, Bettens F & Paepke AJ

MHC-dependent mate preferences in humans

16.20 - 16.40

70

Coenen A

The role of sexual reproduction in the spread of viruses through fungal populations

16.40 - 17.00

317

Sasaki A

Discrete packing of species and taxon cycles

17.00 - 17.20

316

Santucci F, Nascetti G & Bullini L

Genetic structure of the hybridogenetic *Rana esculenta* from Italy

Posters

237 Mitchell SE

Competition and the maintenance of genetic diversity in *Daphnia magna*

378 van Dijk P & Schotman T

The generation of genetic diversity in *Taraxacum officinale*

386 Verdyck P, Dsender K, Grootaert P & Hulselmans J

A comparison of genetic variability between mono- and polyphagous chrysomelid beetles of the genus *Phyllotreta*: a case study of the niche-width variation hypothesis

2) Processes of molecular evolution

John Brookfield, Genetics Dept., Nottingham University,
Queen's Medical Centre, NG7 2UH, UK

Sponsored by the Genetical Society

Appleton Tower Lecture Theatre 4/1

Tuesday

9.30 - 10.00 150 *Chair: JFY Brookfield*
Holland PWH, Garcia
Fernandez J, Williams N,
Sherman A, Patton S &
Shimeld S Homeobox genes and chordate evolution

10.00 - 10.30 13a Averof M & Akam M *Hox* genes and the diversification of insect-
crustacean body plans

10.30 - 11.00 175 King V Evolution of SRY in the Felidae

Coffee

11.30 - 12.00 10 *Chair: JFY Brookfield*
Anxolabhere D &
Nouaud D

12.00 - 12.30 358 Schlotterer C P sequences in *Drosophila*: where did they come
from and where are they going ?
ITS polymorphisms and their meaning for concerted
evolution in *Drosophila melanogaster*

12.30 - 13.00 *General Discussion*

Lunch

14.00 - 14.20 29 *Chair: L Bachmann*
Beye M

14.20 - 14.40 325 Schmid K & Tautz D The homeobox genes *Anip*, *Dfd* and *Sxr* cluster in
the honeybee (*Apis mellifera* L.)

14.40 - 15.00 15 Bachmann L, Venanzetti F Evolutionary divergence of *Drosophila* genes
& Sbordni V Tandemly repeated satellite DNA of *Dolichopoda*
schiazzii: a test for models of the evolution of
highly repetitive DNA

15.00 - 15.20 205 Machado CA, Herre EA & Fig wasps, nematodes and the generation time effect
Birmingham E in molecular evolution

Tea

16.00 - 16.20 186 *Chair: W Stephan*
Koufopanou V, Burt A &

16.20 - 16.40 183 Taylor J Molecular evolution of three fungal proteins

16.40 - 17.00 193 Kostia S, Ruohonen-Lehto Artiodactyl genome fingerprinting by SINE-PCR and
M & Varvio S-L SSR-anchored-PCR

17.00 - 17.20 347 Lachmann M Are random changes the optimal way to change the
DNA ?

Stephan W, Kirby DA & Epistasis and the evolution of compensatory
Muse SV mutations

Wednesday

9.30 - 9.50 289 *Chair: JB Braverman*
Pritchard JK & Schaeffer SW Levels of DNA sequence variation in a *Drosophila*
melanogaster pseudogene provide evidence of linked
directional selection

9.50 - 10.10 44 Braverman JB, Langley CH & Evidence for genetic hitch-hiking at the crest wing
& Aguade M locus of *Drosophila melanogaster*

10.10 - 10.30 163 Jenkins DL, Ortiori CA & A test of adaptive evolution in DNA sequences
Brookfield JFY controlling transcription

10.30 - 10.50 78 Cunningham C, Bull J & Replicable *in vitro* DNA sequence evolution of
Hillis D bacteriophage T7

Posters

2) Processes of molecular evolution

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- | | | |
|-----|-------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------|
| 17 | Bakardjieva NT | Some tendencies in the evolution of enzymes in plants |
| 67 | Cirera S & Aguade M | The sex peptide in <i>Drosophila</i> : evolution at the molecular level |
| 154 | Horak R, Kasak L & Kivisaar M | Mutational processes in nongrowing cells of <i>Pseudomonas putida</i> under stress conditions |
| 204 | Lunadei M, Perani P, Caccio S, Saccone S & Bernardi G | Single-copy sequence homology among the GC-richest isochores of the genomes from cold-blooded vertebrates |
| 220 | Martin Campos JM & Aguade M | Evolution of the <i>Pgd</i> region in <i>Drosophila subobscura</i> : relationship between chromosomal and molecular polymorphism |
| 265 | Varvio S-L & Onkamo P | Microsatellite mutation mechanisms in <i>Artiodactyls</i> : allele sequence differences within and between species |
| 270 | Palo J & Varvio S-L | Moose, <i>Alces alces</i> , lacks microsatellite variation within and between Eurasian and Canadian populations |
| 322 | Scapoli C, Nesti C, Meloncelli D & Barrai I | Asymmetric strand mutation induced by methylases |
| 420 | Yurchenko VY & Kolesnikov AA | The evolution of minicircles in Trypanosomatids |
| 310 | Rozas J & Rozas R | DnaSP, DNA sequence polymorphism: an interactive computer program for estimating population genetic parameters from DNA sequence data |
-

3) Evolution of plant-parasite interactions

Arjen Biere & Joop Ouborg,

Netherlands Inst. of Ecology, P.O.Box 40, NL6666 ZG Heteren, Netherlands

Appleton Tower Lecture Theatre 2

Wednesday

Chair: A Biere

9.30 - 9.40

J Burdon

Introduction

9.40 - 10.20

22

Barrett J

Classic genetic models in coevolution

10.20 - 11.00

335

Simms EL

Costs and benefits of plant response to herbivore and pathogens

Coffee

Chair: A Biere

11.30 - 12.15

102

Ennos R & McConnell KC

Phenotypic variation in plant resistance - implications for pathogen evolution

12.15 - 13.00

49

Burdon J & Ericson L

Metapopulations: an appropriate framework for studying the dynamics of spatially dispersed host-pathogen interactions

Thursday

Chair: J Ouborg

14.00 - 14.30

416

Wool D

The shapes of aphid galls: insect control and/or plant constraints

14.30 - 15.00

382

Vanderberghe F &

Host plant species as a factor influencing genetic

15.00 - 15.30

407

Chavigny P

diversity in populations of aphids *Aphis gossypii*

Interactions between systemic diseases and plants in natural plant populations

Tea

Chair: J Ouborg

16.00 - 16.30

80

Damgaard C & Ostergaard H

Density dependent growth of the barley powdery mildew fungus: infection efficiency and spore production

16.30 - 17.00

30

Biere A & Honders S

Variation in reproductive success of the anther smut fungus *Ustilago violacea* on two related host species, *Silene alba* and *S. dioica*

17.00 - 17.30

268

Ouborg NJ & Mudde CL

Population size, inbreeding and disease susceptibility in the *Silene alba* - *Ustilago violacea* pathosystem

Posters

178 Klein M

Indicators for biotopic management: analyses of the Cynipid *Isocolus scabiosae* galling different host plant structures

258 Nyman T, Roininen H & Vuorinen J

Evolution of different gall types in willow feeding sawflies (Hymenoptera: Tenthredinidae)

261 O'Hara RB & Brown JKM

Frequency and density dependent fitness in the wheat mildew fungus

4) The genetic basis of adaptation and speciation

Peter Keightley, Beate Nürnberger & Michael Whitlock,

ICAPB, Univ. of Edinburgh, West Mains Rd., EH9 3JT, UK

Appleton Tower Lecture Theatre 4

Monday			<i>Chair: B Nürnberger</i>	
9.30 - 10.00	151	Hollocher H	Genetic patterns of sexual isolation in <i>Drosophila melanogaster</i>	
10.00 - 10.30	299	Rieseberg LH	Genic and structural barriers to introgression as revealed by genomic mapping	
10.30 - 11.00	269	Palopoli M & Wu C-I	The genetic basis of hybrid male sterility between <i>Drosophila</i> sibling species: rapidly spinning a complex web of epistasis	
Coffee				
			<i>Chair: P Keightley</i>	
11.30 - 12.00	202	Long AD, Mullaney SL, Reid LA, Langley CH & Mackay TFC	Is standing variation in quantitative traits due to allelic variants at candidate neurogenic loci? Evidence from QTL mapping and quantitative complementation testing in <i>Drosophila</i>	
12.00 - 12.30	319	Kuutinen H & Savolainen O	Genetic basis of flowering time variation	
12.30 - 13.00	209	Mackay TFC, Lyman RF & Fry JD	The genetic basis of quantitative genetic variation: candidate genes and <i>Drosophila</i> bristle number	
Lunch				
			<i>Chair: M Whitlock</i>	
14.00 - 14.20	105	Etges WJ	Genetics of incipient speciation in <i>Drosophila mojavensis</i> : the role of epicuticular hydrocarbons	
14.20 - 14.40	60	Carriere Y & Roff DA	Change in genetic architecture resulting from the evolution of insecticide resistance	
14.40 - 15.00	227	Meagher TR & Costich DE	Nuclear DNA content and floral evolution	
15.00 - 15.20	374	van Delden W & Kamping A	The relationship between latitudinal clines for allozymes, inversions and life history traits in <i>Drosophila melanogaster</i>	
Tea				
			<i>Chair: M Whitlock</i>	
16.00 - 16.20	381	van Tienderen P	Natural variation in flowering time in <i>Arabidopsis thaliana</i>	
16.20 - 16.40	387	Verhoog M, Brakefield P & Holloway GJ	Melanin genes: their effects on fitness	
16.40 - 17.00	194	Lehmann C	Heavy metal tolerance in populations of <i>Calamagrostis epigejos</i> (L.) Roth and <i>Agropyron repens</i> (L.) P. Beauv	
17.00 - 17.20	212a	Mallet J	Mimicry, radiation and speciation in <i>Heliconius</i> butterflies	

Posters

184	Kosuda K	Effect of melanotic tumours on the adult viability of their carriers in <i>Drosophila melanogaster</i>
224	McCabe J & Partridge L	Direct and correlated responses to selection on wing area with constant cell size in <i>Drosophila melanogaster</i>
262	Oka N & Okuyama M	Why have the diving birds been heavily victimized by oil pollution? Aspect of an evolutionary adaptation in nutritive depot structure of diving birds
370	Vakkari P	Industrial melanism of moths in Finland

5) The evolutionary biology of trees and forests

Adrian Newton, IERM, Univ. of Edinburgh, West Mains Rd., EH9 3JU, UK

Appleton Tower Lecture Theatre 2

Monday		<i>Chair: A Newton</i>	
9.30 - 10.00	355	Szmidt A, Wang X-R, Lu M-Z & Parducci L	Population genetic structure of <i>Pinus sylvestris</i> (L.) revealed by analysis of allozyme and RAPD variation: discrepancies and similarities
10.00 - 10.30	336	Sinclair W, Morman J & Ennos R	Mitochondrial markers in native Scots Pine
10.30 - 11.00	126	Gillies ACM, Wilson J & Newton A	An examination of genetic diversity within and between provenances of <i>Cedrela odorata</i> (mahogany) using RAPD markers

Coffee

		<i>Chair: A Newton</i>	
11.30 - 12.00	410	White L & Abernethy K	<i>Aucumea klaineana</i> : a Pleistocene success story now in decline ?
12.00 - 12.30	138	Harris SA	Molecular markers and the study of evolution and systematics in tropical tree legumes
12.30 - 13.00	282	Pennington RT	Phylogenetics of tropical trees: combining molecular and morphological data in <i>Andira</i> (Leguminosae, Dalbergiaceae) to study dispersal biology

Lunch

		<i>Chair: W Sinclair</i>	
14.00 - 14.20	207	Machon N, Godelle B & Gouyon P-H	How did forest trees colonize Europe?
14.20 - 14.40	290	Prus-Glogacki W & Wysocka D	Genetic structure of <i>Pinus mugo</i> Turro populations from the Tatra mountains
14.40 - 15.00	385	Vendramin GG, Vicario F, Lelli L & Rossi P	Genetic relationships among <i>A. alba</i> and the relic population of <i>A. nebrodensis</i> based on RAPD markers and chloroplast DNA variation
15.00 - 15.20	203	Lu M-Z, Szmidt AE & Wang X-R	Molecular characterisation of randomly amplified polymorphic DNAs (RAPDs) in <i>Pinus sylvestris</i>

Tea

		<i>Chair: W Sinclair</i>	
16.00 - 16.20	391	Villani F, Cherubini M, Cesaroni D & Sbordoni V	Geographic variation and genetic structure in natural populations of <i>Castanea sativa</i> Mill. in Turkey
16.20 - 16.40	8	Alstrom-Rapaport C & Gullberg U	Sex ratio and sex determination in the dioecious willow species <i>Salix viminalis</i>
16.40 - 17.00	98	Easton E	Analysis of genetic diversity and clonal spread in discrete populations of aspen (<i>Populus tremula</i> L.) using isozyme analysis

Posters

63	Chevallier M-H & Borgel A	Contribution to the classification of 32 <i>Acacia</i> with reference to their genome size determined by flow cytometry
180	Koelwyn HP, Savolainen O & Koski V	Inbreeding depression in Scots Pine: the later life stages
213	Malvolti ME, Spada M, Beritognolo I & Cannata F	Genetic variability in European naturalised stands of <i>Juglans regia</i> L.
369	Vakkari P & Mattila A	Genetic variation in the stands of English oak (<i>Quercus robur</i>) and European white elm (<i>Ulmus laevis</i>) in Finland

6) Developmental stability

John Manning, Environ. and Evol. Biol., Univ. of Liverpool, PO Box 147, L69 3BX, UK
Anders Pape Møller, Population Biol., Copenhagen Univ., Universitetsparken 15, DK-2100

Appleton Tower Lecture Theatre 1

Monday		<i>Chair: AP Møller</i>	
14.00 - 14.10		Møller AP	Introduction
14.10 - 14.30	42	Brakefield P, Breuker C, Kesbeke F & Saccheri I	Developmental stability, genetics and eyespot formation on <i>Bicyclus</i> wings
14.30 - 14.50	122	Gangstad SW & Yeo DA	Developmental instability and human functional brain asymmetries
14.50 - 15.10	214	Manning JT	Asymmetry and the menstrual cycle in women
15.10 - 15.30	240	Møller AP & Thornhill R	A meta-analysis of the heritability of developmental stability
Tea			
		<i>Chair: AP Møller</i>	
16.00 - 16.20	295	Raymond M, Pontier D, Dufour AB & Møller AP	An evolutionary explanation for human handedness
16.20 - 16.40	353	Swaddle JP	Plumage condition affects flight performance in starlings: implications for developmental homeostasis, abrasion and moult
16.40 - 17.00	361	Thornhill R	Fluctuating asymmetry and honest signalling of phenotypic quality in human sexual selection
17.00 - 17.20	411	Wilkins AS	Gene families, partial functional redundancy and genetic stability
17.20 - 17.30		Møller AP	Conclusion
Tuesday		<i>Chair: JT Manning</i>	
9.30 - 9.50	187a	Kozhara AV	A study of phenotypic variance of bilateral traits in fishes
9.50 - 10.10	278	Passekov V	On the evolutionary stability of ontogenesis in a state-dependent model of Leslie type for a population with age structure
10.10 - 10.30	234	Mignot A, Fessayre A, Godelle B, Dajoz I, Till-Bottraud I & Gouyon P-H	Pollen aperture morphogenesis: what is the range of possible forms?
10.30 - 10.50	7	Alibert P & Auffray J-C	Developmental stability before and after meiotic recombination in subspecific hybrids of European house mice
10.50 - 11.10	306	Rodionova NV	Cellular mechanisms of resorptive processes in the developing skeleton in the different classes of vertebrate

7) **Conflicting and concordant data sets in molecular systematics**

Jeffrey Powell, Biology OML427, Yale University, New Haven CT 06520-8104, USA

Rory Post, Entomology, Wageningen Agric. Univ., Postbus 8031, 6700 EH, Netherlands

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Appleton Tower Lecture Theatre 4

Thursday		<i>Chair: R Post</i>	
9.30 - 10.00	56	Caccone A, Garcia BA & Powell JT	The <i>Anopheles gambiae</i> complex: contrasting phylogenies from nuclear and mitochondrial DNA sequences in mosquitoes
10.00 - 10.30	223	Ruvinsky I & Maxson L	Phylogenetic relationships among families of modern frogs (Bufonidae): insights from mitochondrial gene sequences
10.30 - 11.00	286	Post RJ, Rubio JM & Martin PEM	Evolution of major sperm protein genes in parasitic and other nematodes
Coffee		<i>Chair: R Post</i>	
11.30 - 12.00	320	Sbordoni V	Concordant vs conflicting character sets in systematics: hints from <i>Dolichopoda</i>
12.00 - 12.30	235	Milinkovitch MC, Adachi J, LeDuc R, Farnir F, Georges M & Hasegawa M	A sensitivity approach to character-type weighting and species sampling allows resolution of conflicts in molecular phylogenetic analysis
12.30 - 13.00	330	Sharp P	
Lunch		<i>Chair: V Sbordoni</i>	
14.00 - 14.20	127	Gleason J & Powell JR	A molecular phylogeny of the <i>Drosophila willistoni</i> sibling species based on <i>period</i> , <i>Adh</i> and <i>cytochrome oxidase subunit I</i> DNA sequences
14.20 - 14.40	229	Mes THM & 't Hart H	Cladistic analysis of combined datasets to resolve radiation events in <i>Aeonium</i> (Crassulaceae)
14.40 - 15.00	349	Stevens J & Wall R	Genetic variation in populations of the blowfly <i>Lucilia sericata</i> : mtDNA sequences and RAPD analysis
15.00 - 15.20	275	Pascual M, Balanya J, Latorre A & Serra L	Diagnosis of sibling species of <i>Drosophila</i> by three molecular techniques
Tea		<i>Chair: V Sbordoni</i>	
16.00 - 16.20	111	Flook P & Rowell H	The use of mtDNA sequences for phylogenetic reconstruction of higher order insect relationships
16.20 - 16.40	132	Grau R & Bachmann L	The intergenic spacers of the 5S rDNA genes: a suitable marker for phylogenetic analysis ?
16.40 - 17.00	422	Zhang D-X & Hewitt GM	Insect mitochondrial control region: structure, evolution and usefulness in evolutionary studies
17.00 - 17.20	58a	Carlos J, Oromi P & Hewitt GM	Phylogenetic and population studies on Canadian darkling beetles of the genera <i>Pimelia</i> and <i>Hegeter</i> (Tenebrionidae, Coleoptera) using mtDNA sequences

7) Conflicting and concordant data sets in molecular systematics

Friday			
9.30 - 11.00		<i>R Post</i>	<i>Tour of posters</i>
Coffee			
		<i>Chair: R Post</i>	
11.30 - 11.50	255	Noble LR, Jones CS, Vernon JG & Okamura B	A molecular and morphological investigation of the large anionids (Mollusca: Pulmonata) of NW Europe: identifying friend and foe
11.50 - 12.10	192	Kuusipalo KL	Diversification of endemic Nile Perch <i>Lates niloticus</i> (Centropomidae, Pisces) populations in Lake Tanganyika, east Africa, studied with RAPD-PCR
12.10 - 12.30	287	Pouyand L, Desmarais E, Chenuil A, Bonhomme F & Agnese J-F	Phylogenetic relationships and systematics of the <i>Oreochromis niloticus</i> subspecies complex (Pisces: Cichlidae) with use of microsatellite markers
12.30 - 12.50	123	Gatesy J & Arctander P	Phylogenetic placement of the recently discovered Vu Quang ox based on multiple genetic loci
Lunch			
		<i>Chair: R Crozier</i>	
14.00 - 14.20	76	Crozier RH, Dobric N, Imai HT, Graur D, Coumuet J-M & Taylor RW	Molecular phylogeny of the <i>Myrmecia pilosula</i> group, including ants with the lowest (possible) chromosome number
14.20 - 14.50	103	Emerson BC & Wallis G	The systematics of the New Zealand flightless beetle genus <i>Prodontria</i> with some biogeographic and conservation implications
14.50 - 15.10	211b	Malacrida AR, Guglielmino CR, D'Adam P, Torti C, Marinoni F & Gasperi G	Genetic analysis and phylogenetic inferences among species of Tephritid flies
15.10 - 15.30	279	Paulauskas A, Sruoga A & Mozaliene E	Genetic variety and phylogeny of the Anseriformes order
Tea			
		<i>Chair: R Crozier</i>	
16.00 - 16.20	417	Wuster W & Salamao MG	mtDNA evolution of neotropical pit vipers (<i>Bothrops atrox</i> species group)
16.20 - 16.40	66	Cimaruta R, Forti G, Nascetti G & Bullini L	Reproductive isolation and parapatric habitat displacement between the sibling species <i>Hydromantes ambrosii</i> and <i>H. strinati</i>
16.40 - 17.00	349a	Stewart D, Hoeh R, Sutherland R & Zouros L	Accelerated rates of molecular evolution in the blue mussel, <i>Mytilus</i>
<hr/>			
17.00		<i>International Society of Biochemical Systematics business meeting</i>	

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- | | | |
|-----|--------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 18 | Bandi C, Corona S, Damiani G, Grigolo A, Magrassi L, Sacchi L & Sironi M | Endocytobiosis in cockroaches and termites: a phylogenetic approach |
| 27 | Bensasson D | Using mitochondrial DNA to examine the Pleistocene history of <i>Podisma pedestris</i> |
| 19 | Bianciotti V, Bandi C, Minardi D, Sironi M & Bonfante C | The bacterial endosymbiont of a mycorrhizal fungus belongs to the rDNA group II of Pseudomonads |
| 48 | Buades C, Carrio R, Moya A & Lattore A | Molecular phylogeny of the family Aphididae based on different subunits of the F-ATPase complex |
| 77 | Cuénoud P, Andrews S, Spichiger R & Manen J-M | Preliminary results on the phylogeny and biogeography of the genus <i>Ilex</i> (Aquifoliaceae) |
| 97 | Dijkstra E, Post RJ & de Vryer PW | The choice of DNA sequence for taxonomic studies of planthoppers (Homoptera: Diphacidae) |
| 168 | Jones C, Noble L & Rollinson D | Molecular characterization of the <i>Bullinus forskalii</i> group (gastropoda: Planorbidae) in Cameroon, West Africa; intermediate hosts for <i>Schistosoma</i> spp. |
| 196 | Leskinen E & Pamilo P | Evolution of Baltic Sea <i>Enteromorpha</i> (Chlorophyta) based on nuclear rDNA ITS sequences |
| 217 | Mantovani B, Tinti F, Scali V & Bachmann L | Molecular characterization of the BaB300 satellite DNA family in <i>bacillus</i> stick insects |
| 218 | Marchi A, Addis G & Cmrjar R | Genetic structure and divergence of <i>Polyommatus coridon</i> (Lepidoptera: Lycaenidae) from the island of Sardinia |
| 256 | Said MMS, Noble LR & Craig IW | The amplification and characterization of cholinesterase-like genes in various organisms |
| 272 | Palacios C & Gonzales-Candelas F | Phylogenetic relationships in genus <i>Limonium</i> (Plumbaginaceae) inferred from cpDNA restriction analysis |
| 277 | Passamonti M, Mantovani B & Scali V | Preliminary analysis of satellite DNA in four species of tapetinae (Bivalvia: Veneridae) |
| 315 | Santucci F, Cicolani B, Andreani P & Bullini L | Preliminary data on genetic differentiation between freshwater crayfish |
| 321 | Venzanetti F, Bachmann L & Sbordoni V | Highly repetitive satellite DNA as a molecular marker for phylogenetic analyses of the genus <i>Dolichopoda</i> |
| 345 | Stauffer C & Lakatos F | Phylogenetic relationship of the European <i>Ips</i> De Geer bark beetles (Coleoptera, Scolytidae): a mitochondrial DNA and allozyme analysis |
| 368 | Vachot A-M & Monnerot M | Access to museum collections for evolutionary studies |
| 372 | van de Peer Y & de Wachter R | TREECON for Windows: a software package for the construction and drawing of evolutionary trees for the Microsoft Windows environment |
| 373 | van de Peer Y, van der Auwera G & de Wachter R | The evolution of stramenopiles and alveolates based on small ribosomal subunit RNA taking into account nucleotide variability |
| 375 | van der Auwera G, de Rijk P & de Wachter R | The phylogeny of the mastigomycetes as inferred from large ribosomal subunit RNA sequences |
| 302 | Rey I, Arano B & Machordom A | When explosive chromosome divergence does not run parallel to genic differentiation: the case of the fossorial rodents of the genus <i>Ctenomys</i> |
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8) Behaviour and evolution

Linda Partridge, Genetics & Biometry, University College London,
4 Stephenson Way, NW1 2HE, UK

George Square Lecture Theatre

Tuesday		<i>Chair: L Partridge</i>	
14.00 - 14.45	273	Parker G	Sperm competition games
14.45 - 15.30	173	Keller L	Evolution of partitioning of reproduction in animal societies
Tea			
		<i>Chair: L Partridge</i>	
16.00 - 16.45	89	Dias P & Blondel J	Adaptation and local maladaptation in Mediterranean blue tits
16.45 - 17.30	2	Alatalo R	Evolution of lekking behaviour
Wednesday		<i>Chair: B-E Saether</i>	<i>Life history evolution</i>
9.30 - 9.50	153	Horak P	Selection on female phenotypic quality in the Great Tit
9.50 - 10.10	169	Joensson KI, Tuomi J & Järmo J	The consequences of pre- and post-breeding costs of reproduction on the evolution of reproductive effort tactics
10.10 - 10.30	312	Saether B-E, Andersen R & Torkild Tveraa T	How do long-lived seabirds avoid over-investing in their offspring?
10.30 - 10.50	331	Sheldon B, Gustafsson L & Quarnstrom A	Trade-offs between life history traits and sexual ornaments
Coffee		<i>Chair: P Forslund</i>	<i>Parasitism</i>
11.30 - 11.50	113	Forslund P	Intraspecific nest parasitism in the barnacle goose: behavioural tactics of parasites and hosts
11.50 - 12.10	341a	Soler JJ & Moller AP	Cuckoo host selection: characteristics determining the selection of the host by the European cuckoo (<i>Cuculus canorus</i>)
12.10 - 12.30	348	Stern DL	Phylogenetic evidence that aphids, rather than plants, determine gall morphology
12.30 - 12.50	39	Boulinier T, Monnat J-Y & Danchin E	Ectoparasitism as a factor of habitat selection in a colonial bird
Thursday		<i>Chair: S Parri</i>	<i>Sexual selection</i>
9.30 - 9.50	71	Cook J, West S & Compton S	Male dimorphism, alternative mating strategies and virginity in fig wasps
9.50 - 10.10	145	Hellriegel B & Ward PI	Sperm competition in the yellow dung fly <i>Scathophaga stercoraria</i> : adding the female perspective
10.10 - 10.30	185	Kotiaho J	Sexual selection in a wolf spider: male drumming activity, body size and viability
10.30 - 10.50	274	Parri S	Female preferences for male drumming signals in a wolf spider <i>Hygrolycosa rubrofasciata</i>
Coffee		<i>Chair: M Kirkpatrick</i>	<i>Sexual selection</i>
11.30 - 11.50	176a	Kirkpatrick M	Evolution of mating preferences for male genetic quality
11.50 - 12.10	82	Dawson K	Evolutionary consequences of a trade-off between parental effort and mating effort
12.10 - 12.30	305	Ritchie MG	The "shape" of female mating preferences in a bushcricket
12.30 - 12.50	210	Mackenzie A, Reynolds J & Sutherland W	Assessing potential sexual selection on leks

8) Behaviour and evolution

Thursday		<i>Chair: RA Johnstone</i>	<i>Evolutionarily stable strategies</i>
14.00 - 14.20	137a	Hammerstein P	Phenotypic and genetic approaches to evolution; a new synthesis?
14.20 - 14.40	246	Nagelkerke CJ	Hierarchical levels of spatial structure and their consequences for the evolution of sex allocation in mites and other arthropods
14.40 - 15.00	409	West S & Flanagan K	Simultaneous optimisation of sex allocation and clutch size
15.00 - 15.20	167	Johnstone RA	Multiple displays in animal communication
15.20 - 15.40	253	Nishimura K & Yamakita N	Evolution of cannibalism: a simple strategy model in the view of parental control
Tea			
		<i>Chair: T Boulinier</i>	<i>Ecology</i>
16.00 - 16.20	86	De Meester L, Weider LJ & Tollrian R	Diel vertical migration and size-dependent habitat partitioning in <i>Daphnia</i> : a tower experiment on the impact of fish predation on clonal existence
16.20 - 16.40	291	Pulido F & Berthold P	Relationship between incidence and amount of migratory activity in the blackcap (<i>Sylvia atricapilla</i>) - consequences for the evolution of sedentarity in a migratory bird species
16.40 - 17.00	356a	Taneyhill D	Rules and mechanisms in the evolution of foraging behaviour
Friday		<i>Chair: A Sih</i>	<i>Colours</i>
9.30 - 9.50	215	Mappes J & Alatalo R	Synergistic selection on warning coloration: experiments with traditional and novel signal
9.50 - 10.10	114	Forsmann A	Opposing fitness consequences of colour pattern in male and female snakes
10.10 - 10.30	334	Sih A & Storfer A	The evolution of ineffective antipredator behaviour in a sunfish-salamander system
10.30 - 10.50	341	Smithson A & Macnair MR	Frequency-dependent fitness and the evolution of floral traits through pollinator behaviour patterns
Coffee			
		<i>Chair: L Witting</i>	<i>Ecology</i>
11.30 - 11.50	115	Frischknecht M	Predators choosing between patches with a standing crop: the influence of learning rules and input types
11.50 - 12.10	413	Witting L	The body mass allometries as evolutionarily determined by the foraging process of mobile organisms
12.10 - 12.30	285a	Popovkina A	Behavioural changes in Ruddy Shelducks (<i>Tadorna ferruginea</i> Pall.) of the Askania-Nova population
12.30 - 12.50	393	Vogl C & Grillitsch B	Quantification of swimming behaviour of fish with an automated videomonitoring system

8) Behaviour and evolution

Friday		Chair: JJ Boomsma	Social evolution
14.00 - 14.20	36	Boomsma JJ	Queen-male conflict over mating in eusocial hymenoptera: eager females and reluctant males?
14.20 - 14.40	106	Fjerdingstad EJ, Boomsma JJ, Thoreu P & Paxton RJ	Patterns of polyandry in the leafcutter ant <i>Atta columbica</i> - microsatellite genetic data and sperm counts compared
14.40 - 15.00	280	Paxton RJ, Thoren P, Tengo J & Estoup A	Genetical relatedness in a communal bee using microsatellite loci
15.00 - 15.20	243	Moritz RFA & Schmitz J	Sociality and the rate of evolution in social wasps
Tea		Chair: E Svensson	Sex allocation
16.00 - 16.20	352	Svensson E & Nilsson J-A	Mate quality affects offspring sex ratio in the blue tit (<i>Parus caeruleus</i>)
16.20 - 16.40	314	Sandell M	Female-female competition and the role of females in influencing mating systems
16.40 - 17.00	339	Smith HG & Wennerberg L	Paternity and paternal care in polygynous European starlings
17.00 - 17.20	351	Sundstrom L & Chapuisat M	Facultative sex ratio biasing in ants
17.20 - 17.40	398	Walsh L & Seppa P	Sex allocation of the two forms of <i>Myrmica ruginodis</i> (Hymenoptera, Formicidae)

Posters

34	Blier P & Lemieux H	Energetic metabolism and habitat competition in <i>Nereis virens</i>
244	Mouritsen KN	Crawling behaviour in <i>Macoma balthica</i> : the parasite-manipulation hypothesis revisited
61a	Chapman T, Gray N & Partridge L	Nutrition, age at reproduction and the cost of mating in female <i>Drosophila melanogaster</i>
219	Marrow P, Stevenson IR, Clutton-Brock TH, Houston AI & McNamara JM	Reproductive decisions and life history tactics in Soay sheep
254	Noach EJK, de Jong G & Scharloo W	Locomotor activity in selection lines of <i>Drosophila melanogaster</i>
328	Sella G, Besostri Grimaldi B, Premoli MC & Ramella L	Sex ratio and local mate competition in <i>Dinophilus gyrocallatus</i>
112	Forchhammer MC & Boomsma JJ	Wait or wander: the evolution of mating system in musk oxen
220a	Martinez JG, Soler M & Soler JJ	Egg destruction by great spotted cuckoos: adaptation or exaptation?
125	Gertsch P & Fjerdingstad EJ	Efficiency of detecting multiple inseminations in ants at different levels of sperm bias using microsatellite markers
133	Grootaert P	Male secondary sexual characters and sexual selection in the wine fly genus <i>Cynrotopus</i> (Insecta, Diptera, Dolichopodidae)
337	Skarstein F & Folstad I	On sperm and the immunocompetence handicap

9) Evolution of life cycles and mating systems

Richard Ennos, IERM, Univ. of Edinburgh, West Mains Rd., EH9 3JU, UK

Sarah Otto, ICAPB, Univ. of Edinburgh, West Mains Rd., EH9 3JT, UK

Rolf Hoekstra, Genetics, Wageningen Univ., Dreijenlaan 2, NL6703 HA Wageningen, Netherlands

Appleton Tower Lecture Theatre 3

Monday

Chair: RF Hoekstra

14.00 - 14.30 25

Bell G

Comparative biology of life cycles in seaweeds

14.30 - 15.00 148

Hoekstra RF

Evolutionary biology of fungi: promises and problems

15.00 - 15.30 129

Goff L

The evolution of parasitism in red algae

Tea

Chair: RF Hoekstra

Algae

16.00 - 16.30 267

Otto SP

What population genetic models predict about the distribution of haploidy and diploidy

16.30 - 17.00 87

De Visser A, Hoekstra RF & Van den Ende H

Deleterious mutations and the ecology of sex in *Chlamydomonas*

17.00 - 17.30 401

Wattier R, Destombe C, Valero M, Dallas J & Veuille M

Population genetic structure of a haplo-diploid red seaweed *Gracilaria verrucosa*: within population microdifferentiation and breeding system

Tuesday

Chair: F Debets

Fungi

9.30 - 10.00 88

Debets F

The dynamics of mitochondrial plasmids in a Hawaiian population of *Neurospora intermedia*

10.00 - 10.30 293

Ramsdale M & Rayner ADM

Relationships between genomic conflict and phenotypic instability following sympatric and allopatric matings in basidiomycete fungi

10.30 - 11.00 247

Nauta M

Is the highly polymorphic vegetative incompatibility system selectively neutral?

Coffee

Chair: SP Otto

11.30 - 12.00 31

Biermann CH

Gamete recognition and molecular variation in circumarctic sea urchins (Echinoidea: Strongylocentridae)

12.00 - 12.30 53

Burt A, Carter DA, Koenig GL, White TJ & Taylor JW

Molecular markers reveal cryptic sex in the human pathogen *Coccidioides immitis*

12.30 - 13.00 85

De Haan A & Van Damme JMM

The maintenance of male sterility

Lunch

Chair: X Vekemans

14.00 - 14.20 256a

Noirot M

Evolutionary potentialities in agamic complex: old and new concepts

14.20 - 14.40 222

Maurice S

The effect of pollen limitation on plant reproductive systems and the maintenance of sexual polymorphism

14.40 - 15.00 344

Staedler T

Gene silencing and mating system evolution in polyploid hermaphrodites

15.00 - 15.20 384

Vekemans X

Inference on ancient population genetic parameters from sequence data on multiallelic mating system loci in plants: a dream or reality?

Tea

Chair: NK Michiels

16.00 - 16.20 93

Doums C, Delay B & Jarne P

The evolution of phally polymorphism in the hermaphrodite freshwater snail *Bulinus truncatus*: genetic variation of the aphally frequency within and between populations

16.20 - 16.40 233

Michiels NK, Weinzierl RP & Streng A

Sperm exchange in the planarian flatworm *Dugesia polychroa*, a simultaneous hermaphrodite: do they trade?

16.40 - 17.00 189

Kraak SBM & de Looze EMA

A new hypothesis on the evolution of sex determination in vertebrates; big females ZW, big males XY

10) Complex dynamics and evolution

Michael Doebeli, Zoology Institute, Univ. of Basel, Rheinsprung 4, CH-4051 Basel, Switzerland
Appleton Tower Lecture Theatre 3

Wednesday		<i>Chair: M Doebeli</i>		<i>The evolution of population dynamics</i>	
9.30 - 10.00	392	Visser ME, Rohani P & Driessen G		Ecological versus evolutionary stability: does natural selection promote persistence of host-parasitoid interactions?	
10.00 - 10.30	128	Godfray HCJ, Briggs CJ & Wilson HB		Joint evolutionary and population dynamics in insect-natural enemy interactions	
10.30 - 11.00	195	Lenski R & Travisano M		Dynamics of adaptation and diversification: a 10,000 year experiment with bacteria	
Coffee		<i>Chair: M Doebeli</i>			
11.30 - 12.00	294	Rand DA		Evolutionary dynamics of some spatially extended individual-based systems	
12.00 - 12.30	107	Ferriere R & Gatto M		Protective chaos favored by natural selection in metapopulations	
12.30 - 13.00	230	Metz H		Adaptive dynamics and evolutionarily singular strategies: geometrical consequences of nearly faithful reproduction	
Thursday		<i>Chair: J Koella</i>			
9.30 - 9.50	83	De Jong G		Genotypic demography: simultaneous dynamics of numbers and allele frequencies	
9.50 - 10.10	414	Witting L		Population dynamics by density dependent life-history evolution	
10.10 - 10.30	371	van Baalen M & Sabelis MW		Non-equilibrium dynamic of 'ideal and free' prey and predators	
10.30 - 10.50	179	Koella J & Doebeli M		The evolution of simple population dynamics	
Coffee		<i>Chair: C Cannings</i>		<i>Game theory</i>	
11.30 - 11.50	28	Bergstrom CT, Godfrey-Smith P & Lachmann M		Competition between pure and mixed strategists in evolutionary games	
11.50 - 12.10	58	Cannings C, Broom M & Vickers GT		Evolutionary conflicts with multiple constraints	
12.10 - 12.30	45a	Broom M, Cannings C & Vickers G		A sequential arrivals model of territory acquisition	
12.30 - 12.50	379	van Dooren T, Metz JAJ & Matthysen E		Delayed maturation in semelparous populations with non-equilibrium dynamics	
Friday		<i>Chair: R Bürger</i>		<i>Quantitative genetics</i>	
11.30 - 11.50	281	Peck JR & Barreau G		Genetic drift and the evolution of sex	
11.50 - 12.10	52	Bürger R		The distribution of quantitative traits under mutation, selection and drift	
12.10 - 12.30	75	Crnokrak P & Roff DA		Dominance variance: associations with selection and fitness	
12.30 - 12.50	356	Tanaka Y & Roff DA		The maintenance of alternative phenotypes by threshold selection, mutation and drift	
Lunch		<i>Chair: JR Peck</i>		<i>Origins</i>	
14.00 - 14.20	244a	Muller AWJ		Were the first organisms heat engines? A new paradigm for the origin of life and early evolution	
14.20 - 14.40	161	Jako E		Transfer RNA identity in mathematical logical language	
14.40 - 15.00	365	Ujhelyi M		Some thoughts about the origins of syntax	
Tea		<i>Chair: T Kawecki</i>		<i>Speciation</i>	
16.00 - 16.20	172	Kawecki T		Can mutations drive sympatric speciation?	
16.20 - 16.40	92	Doebeli M		A quantitative genetic model for sympatric speciation	
16.40 - 17.00	292	Pykov K		A multilocus model of the selection barrier between populations	
17.00 - 17.20	90	Dieckmann U		The dynamical theory of coevolution - a unifying perspective	
17.20 - 17.40	130a	Gorshkov A & Makareva AM		The new explanation of Haldane's Rule	

Posters

10) Complex dynamics and evolution

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|------|--------------------------------------|-------------------------------------------------------------------------------------------------------------------|
| 11 | Aparici Sanz E, Carmona MJ & Serra M | Proportion among bisexually-reproducing individuals in populations of monogonont rotifers: a theoretical approach |
| 21 | Barreau G & Peck JR | Fisherian mutations, epistasis and the transition from sexuality to asexuality |
| 268a | Ovsynnikov L & Passekov B | Evolution of a resource-consumer community with an account of the genetic structure of the consumer population |

11) The evolution of plasticity

Mark Kirkpatrick, Zoology, Univ. of Texas, Austin, TX 78712, USA

Gerdien de Jong, Vakgroep Populatie- en Evolutiebiologie,

Universiteit Utrecht, Padualaan 8, NL-3584 CH Utrecht, Netherlands

Appleton Tower Lecture Theatre 5/1

Monday			<i>Chair: M Kirkpatrick</i>	<i>The evolution of plasticity</i>
9.30 - 10.00	177	Kirkpatrick M		Plasticity: what is it, and what is it good for?
10.00 - 10.30	43	Brakefield P, Kesbeke F & Koch PB		Interactions between morphological and life history traits and the evolution of plasticity in tropical butterflies
10.30 - 11.00	346	Stearns SC & Kaiser M		Rapid evolution of an induced life history response
Coffee			<i>Chair: D Bourguet</i>	<i>The genetics of plasticity</i>
11.30 - 11.50	40	Bourguet D, Prout M & Raymond M		Dominance level influenced by environmental conditions
11.50 - 12.10	307	Roff D		The evolution of genetic correlations: an analysis of patterns
12.10 - 12.30	412	Windig JJ		How to analyse the genetics of phenotypic plasticity?
12.30 - 12.50	380	van Hinsberg A		Responses and correlated responses to artificial selection on leaf length in <i>Plantago lanceolata</i> L.
Lunch			<i>Chair: JR David</i>	<i>Development, physiology and morphology</i>
14.00 - 14.20	14	Azevedo R, James AC & Partridge L		Geographic variation in phenotypic plasticity of wing area and its cellular basis in <i>Drosophila melanogaster</i>
14.20 - 14.40	162	James AC, Azevedo RBR & Partridge L		Phenotypic plasticity of development time and body size in <i>Drosophila melanogaster</i>
14.40 - 15.00	81	David JR, Gibert P, Mretau B, Morin JP & Petavy G		Evolution of reaction norms in <i>Drosophila</i> : results of a comparative approach among species
15.00 - 15.20	266	Ottenheim MM & Holloway GJ		Wing load plasticity in <i>Eristalis arbustorum</i> (Diptera: Syrphidae)
Tea			<i>Chair: D Roff</i>	<i>Development, physiology and morphology</i>
16.00 - 16.20	120	Galis F		Developmental plasticity and the facilitation of evolutionary changes
16.20 - 16.40	298	Reig S, Doadrio I & Mironovsky A		Geometric analysis of size and shape variation in barb morphotypes from Lake Tana (Ethiopia)
16.40 - 17.00	357	Tarasjev A		Phenotypic plasticity in <i>Iris pumila</i> - spatial and temporal aspects
17.00 - 17.20	159	Jablonka E, Oborny B, Molnar I, Kisdi E, Hofbauer J & Czaran T		Phenotypic plasticity and carry-over effects
17.20 - 17.40	225a	McWatters H & Saunders D		Geographic variation in diapause in the bluebottle <i>Calliphora vicina</i>
Tuesday			<i>Chair: G de Jong</i>	
9.30 - 10.00	84	De Jong G		The evolution of phenotypic plasticity in an unpredictable environment
10.00 - 10.30	405	Weis AE & Brown DG		Plant defense as a system of cascading reaction norms
10.30 - 11.00	343	Spitze K		Evolution of a generalist genotype: assessing the adaptiveness of phenotypic plasticity
Coffee			<i>Chair: J. Kozlowski</i>	<i>Allocation of resources</i>
11.30 - 11.50	34a	Boersma M		The allocation of resources to reproduction in <i>Daphnia</i>
11.50 - 12.10	108	Flanagan K & West S		Sex allocation in response to varying host size in the parasitoid, <i>Achrysocharoides zweelferi</i> ; a field study
12.10 - 12.30	182	Koskela E		The trade-off between litter size and offspring viability
12.30 - 12.50	188	Kozlowski J		Optimal allocation of resources explains Charnov's life history invariants for indeterminate growers

11) The evolution of plasticity

Tuesday

*** Move to Lecture Theatre 1 ***

Chair: A Lomnicki

14.00 - 14.20 216 Mappes T, Koskela E & Ylönen H

14.20 - 14.40 100 Ellers J

14.40 - 15.00 283 Perrin N

15.00 - 15.20 200 Lomnicki A

15.20 - 15.40 342 Sorci G & Clobert J

Plasticity in life histories

Reproductive costs and offspring survival in relation to litter size

Life history evolution in the parasitoid *Asobara tabida*

Life-history responses to predation in *Physa acuta* (Gastropoda)

Does reduced selection pressure on *Tribolium confusum* in a favorable environment decrease their fitness in this environment?

Phenotypic plasticity of growth and survival in the common lizard (*Lacerta vivipara*)

Tea

Chair: G Sorci

16.00 - 16.20 402 Weber A

16.20 - 16.40 33 Blarer A, Doebeli M & Stearns SC

16.40 - 17.00 201 Lomónaco C, Gorur G & Mackenzie A

17.00 - 17.20 268b Ovsysnnikov L

Plasticity in life histories

Microevolutionary processes in *Daphnia* due to predators

Pitfalls in diagnosing ageing from patterns of mortality and fecundity

Phenotypic plasticity in fitness and morphological traits of the black bean aphid *Aphis fabae* reared on different host plants

Evolutionary optimal values of swimming velocity and fertility of pelagic fish: correlation between energy expenses for various kinds of vital activity

Posters

131 Gorur G Lomonaco C & Mackenzie A

110 Fleming IA, Jonsson N & Jonsson B

116 Fry JD, Lee S & Mackay TFC

117 Boriss H & Gabriel W

304 Rispe C, Simon JH-C & Pierre J-S

301 Repka S & des Forges C

338 Smekens MJE

367 Uotila LA & Niemela M

Phenotypic plasticity in aphids in response to host plants and secondary chemicals

Phenotypically plastic response of egg production to early growth in Atlantic salmon

The contribution of new mutations to genotype-environment interaction for fitness in *Drosophila melanogaster*

The selective advantage of phenotypic plasticity in vertical migration of *Daphnia* in a competition and predation structured community

What to do when selection fluctuates: gamble, save or both?

Inter- and intraspecific differences of *Daphnia* life histories in response to two food sources,

Scenedesmus and *Oscillatoria*

Salt adaptation in a constant or (temporally or spatially) varying environment

Plasticity in reproductive tactics in a freshwater colonial animal

12) Selfish genetic elements

Ian Hastings, ICAPB, Univ. of Edinburgh, West Mains Rd., EH9 3JT, UK
 Rolf Hoekstra, Genetics Dept., Wageningen Agricultural University,
 Dreijenlaan 2, NL6703 HA Wageningen, Netherlands

Appleton Tower Lecture Theatre 1

Friday		<i>Chair: I Hastings</i>	
9.30 - 10.15	38	Bougard S	B chromosomes: a classic case of selfish genetic elements
10.15 - 11.00	354	Szathmary E	Selfishness and the integration of genetic information during evolutionary transitions
Coffee		<i>Chair: I Hastings</i>	
11.30 - 11.50	421	Zeyl C & Bell G	The spread of a retrotransposon in sexual and asexual populations of yeast
11.50 - 12.10	152	Hoogland C & Biemont C	Distribution of transposable elements along the polytene chromosomes of <i>Drosophila melanogaster</i> : test of the ectopic recombination model for maintenance of insertion site number
12.10 - 12.30	390	Vieira C & Biemont C	Selection against transposable element insertions is stronger in <i>Drosophila simulans</i> than in <i>D. melanogaster</i>
12.30 - 12.50	211a	Malacrida AR, Torti C, Costi S & Gasperi G	Germline and somatic instability in the medfly <i>Ceratitis capitata</i> (Diptera, Tephritidae)
Lunch		<i>Chair: G Bell</i>	
14.00 - 14.20	415	Witting L	Selfish genetic elements as the optimal genetic code
14.20 - 14.40	5	Albert B	Evolution of plant mitochondrial genome: model of a three-level selection process

Posters

376	van der Gaag M & Hoekstra RF	Population genetic aspects of spore killing in <i>Podospira anserina</i>
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13) Chromosome variation and evolution

Jeremy Searle & Heidi Häuffe, Biology, Univ. of York, Heslington, YO1 5DD, UK

Appleton Tower Lecture Theatre 1

Thursday

9.30 - 10.00	423	<i>Chair: H Häuffe</i> Zima J, Rab P, Macholan M & Phillips RB	Chromosomal evolution in the mammals and fishes of Europe
10.00 - 10.30	9	Angus RB	The use of chromosomes to elucidate biogeography and speciation patterns in water beetles

10.30 - 11.00

Coffee

11.30 - 12.00	164	<i>Chair: H Häuffe</i> Jenkins G	Structural divergence of chromosomes and its effect upon meiosis
12.00 - 12.30	45	Britton-Davidian J, Fel F, Caalan J & Fillon V	Chromosomal clines in the Danish hybrid zone between European house mice
12.30 - 13.00	221	Mason P, Serrano L, Bella JL, de la Torre J, Lopez-Fernandez C, Garcia de la Vega C, Buno I, Torreja E & Gosalvez J	Population cytogenetics of a hybrid zone in the grasshopper <i>Chorthippus parallelus</i>

Lunch

14.00 - 14.20	394	<i>Chair: J B Searle</i> Volobouev V, Vogt V, Malfoy B & Luttriaux B	Repeated DNAs and chromosome evolution in three <i>Gerbillus</i> species
14.20 - 14.40	400	Warburton P, Haaf T, Gosden J & Willard H	Non-orthologous evolution of alpha satellite DNA at the centromeres of humans and the great apes
14.40 - 15.00	176	Kipling D, Mitchell AR & Cooke HJ	Functional organization of mouse centromeres - implications for evolution
15.00 - 15.30		<i>Discussion</i>	DNA structure and chromosomal evolution

Tea

16.00 - 16.20	396	<i>Chair: J B Searle</i> Vysotskaya LV	Robertsonian fusions, heterochromatin and chiasma distributions in the karyotype evolution of grasshoppers
16.20 - 16.40	288	Price DJ & Sands DD	A review of the chromosomes of <i>Corydoras</i> catfishes, with a preliminary report on <i>C. adolfi</i> and <i>C. imitator</i> , sympatric species from a tributary of the upper Rio Negro
16.40 - 17.00	72	Cook L	Extraordinary karyotypic variation in <i>Apiomorpha</i> : is chromosomal evolution driving speciation?
17.00 - 17.30		<i>Discussion</i>	General discussion on chromosomal variation and evolution

Posters

13) Chromosome variation and evolution

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|------|------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------|
| 51 | Bugrov AG | Sex-chromosome polymorphism and cytogenetics of interpopulation hybrids in the grasshopper <i>Podisma sapporensis</i> Shir. |
| 94 | Ducroz J-F, Granjon L & Volobuev V | Chromosomal, molecular and reproductive evidence for the presence of two distinct species of <i>Arvicanthis</i> (Rodentia, Muridae) in West Africa |
| 119 | Galleni L, Telim A, Stanyon R & Contadini L | Sex chromosome evolution and speciation: the case of the Savi pine vole, <i>Microtus savii</i> (Rodentia, Arvicolidae) |
| 134 | Grozeva S & Maryanska-Nadachowska A | Polymorphic sex chromosome mechanism in two species of <i>Cacopsylla</i> (Homoptera, Psyllidae) |
| 141 | Hauffe HC & Searle JB | Fertility of house mice from a chromosomal hybrid zone in the Italian Alps |
| 276 | Mestres F, Sanz J, Pascual M & Serra L | Lack of recombination between chromosomal arrangements in <i>Drosophila subobscura</i> |
| 61b | Charalambous M, Shelley AJ, Maia-Herzog M & Lima-Dias APA | Chromosomal variation in the blackfly onchocerciasis vector <i>Simulium guianense</i> in Brazil |
| 313 | Said K, Chatti N, Benzekri K, Auffray J-C & Britton-Davidian J | Fluctuating asymmetry in the chromosomal races of house mouse in Tunisia and their hybrids |
| 327 | Sella G, Vitturi R, Columba MS, Protto P, Quaranta S & Ramella L | Nucleolus organizer regions and karyotypic evolution in the genus <i>Ophryotrocha</i> (Polychaeta) |
| 418 | Wytenbach A | Genetic structuration on a microgeographic scale: implications for the fixation of chromosomal mutants in <i>Sorex araneus</i> (Mammalia, Insectivora) |
| 232 | Michailova P, Petrova N, Ramella L, Sella G & Todorova D | Effects of pollution on the polytene chromosomes of <i>Chironomus riparius</i> Meigen 1804 (Chironomidae, Diptera) from a river Po station |
| 274a | Pascoe PL & Dixon DR | Karyotype evolution and genome size in muricid gastropods |
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14) Interactions between parasite transmission and sexual strategy

Jacqui Shykoff, Experimental Ecology, ETH Zurich, ETHZ - NW, CH-8092 Zürich, Switzerland

Alison Dunn, Pure & Applied Biology, Univ. of Leeds, LS2 9JT

Gregory Hurst, Genetics, Cambridge University, Downing St., CB2 3EH, UK

George Square Lecture Theatre/Appleton Tower Lecture Theatre 3

Tuesday

Chair: A Dunn

- 9.30 - 10.00 408 Werren JH
- 10.00 - 10.20 37a Bouchon D Rigaud T & Juchault P
- 10.20 - 10.40 303 Rigaud T, Bouchon D & Juchault P
- 10.40 - 11.00 284 Poinot D & Mercot H

Evolution of *Wolbachia*: bacteria that alter reproduction in arthropods
Molecular diversity of *Wolbachia*, endosymbionts of Crustaceans
Are interspecific horizontal transfers effective for *Wolbachia* propagation in isopods?
Wolbachia infection in *Drosophila simulans*: does the bacteria modify the fitness of its host?

Coffee

Chair: J Shykoff

- 11.30 - 12.00 318 Saul GB
- 12.00 - 12.30 324 Schilthuizen M & Stouthammer R
- 12.30 - 12.50 206 Machkevsky VK

Characteristics of cytoplasmic cross incompatibility in the parasitoid wasp *Nasonia* (= *Mormoniella*) *vitripennis*
Host shifts in parthenogenesis-causing bacteria
Sexual strategy of the trematode *Proctoeces maculatus* Odhner, 1911 in support of their population structure

Thursday

*** Move to Lecture Theatre 1 ***

Chair: L Groves

- 14.00 - 14.30 139 Hatcher MJ, Dunn AM & Tofts C
- 14.30 - 14.50 96 Dunn A, Hatcher M, Tofts C & Terry R
- 14.50 - 15.10 1 Agnew P & Koella JC
- 15.10 - 15.30 135 Groves L, Read AF & Wallier D

Evolutionary interactions between cytoplasmic sex ratio distorters, host fitness and sex ratio
Strategies of transovarial transmission by a microsporidian sex ratio distorter in *Gammarus duebeni*
Virulence and parasite transmission route: a protozoan Jekyll and Hyde
Transmission dynamics of malaria parasites

Tea

Chair: P Kover

- 16.00 - 16.30 332 Sheldon B
- 16.30 - 17.00 155/211 Hurst G & Majerus M
- 17.00 - 17.20 359 Thomas F, Renaud F, Demeus T, Cezilly F & Rousset F
- 17.20 - 17.40 187 Kover PX & Clay K

Evolutionary consequences of sexually transmitted diseases for host reproductive strategies
Parasites, age and sexual selection
RAPD markers indicate that horizontal transmission is the predominant mode of transmission in the mixed strategist *Atkinsonella hypoxylon*

Posters

- 377 van Diepeningen AD *Aspergillus niger* and its viruses
- 32 Bigliardi E, Biscaldi G, Corona S, Grigolo A, Laudani U, Sacchi L & Selmi MG Endocytobiosis in cockroaches and termites: a morphological approach
- 210a MacKinnon MJ & Hastings IM Evolution of drug resistance in the malarial parasite IM

15) Evolutionary radiations and development

Euan Clarkson, Geology Dept., Univ. of Edinburgh, West Mains Rd., EH9 3JW, UK

Richard Bateman, Royal Botanic Gardens, 20A Inverleith Row, Edinburgh, UK

Appleton Tower Lecture Theatre 2

Tuesday			<i>Chair: ENK Clarkson</i>	
9.30 - 10.00	3	Ahlberg PE		Conceptual leaps and morphological jumps: a coelacanth case study
10.00 - 10.30	23	Bateman RM		Explaining higher plant radiations: do radical developmental mutations drive phylogenetic change across fitness seascapes?
10.30 - 11.00			<i>General discussion</i>	
Coffee				
			<i>Chair: R Bateman</i>	
11.30 - 12.00	68	Clarkson ENK & Taylor CM		Heterochrony and evolutionary change in upper Cambrian Olenid trilobites
12.00 - 12.30	340	Smith AB		Evolutionary radiations in echinoderms: a comparison of larval and adult diversification
12.30 - 13.00	104a	Erwin DH, Valentine JW & Jablonski D		The developmental evolution of metazoan body plans: the fossil evidence
Lunch				
			<i>Chair: ENK Clarkson</i>	
14.00 - 14.20	4	Alberch P		Exaptation and the intra-population and intra-specific evolution of viviparity in the urodele <i>Salamandra salamandra</i>
14.20 - 14.40	79	Dajoz I, Vincent M & Till-Bottraud I		Pollen heteromorphism, flower morphology and pollinator behaviour: a correlation
14.40 - 15.00	99	Eble GJ		Testing the role of development in evolutionary radiations
15.00 - 15.20	121	Galis F		New insights on a key evolutionary innovation
Tea				
			<i>Chair: R Bateman</i>	
16.00 - 16.20	236	Fusco G & Minelli A		Morphological vs developmental complexity in centipedes
16.20 - 16.40	300	Renaud S, Jaeger J-J & Auffray J-C		Uncoupled patterns of size and shape evolution in a fossil rodent (<i>Stephanomys</i>): a Fourier analysis approach
16.40 - 17.00	399	Wall R & Stevens J		Radiation and classification of the blowfly genus <i>Lucilia</i> (Diptera: Calliphoridae)

Posters

144	Helgason T & Knapp S	Seed structure and group delimitation in <i>Solanum</i> sect. <i>Pteroleia</i> Dunal
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16) Current topics in population structure

Phil Hedrick, Zoology, Arizona State Univ., Tempe, AZ 85287, USA

Appleton Tower Lecture Theatre 5

Tuesday		<i>Chair: P Hedrick</i>	
14.00 - 14.30	199	Loeschke V & Hansen MM	Discordance of population structure as revealed by different genetic markers
14.30 - 15.00	271	Pamilo P	Spatial structure of social insect populations
15.00 - 15.30	319a	Savolainen O, van Treuren R, Karkkainen K & Karhu A	Spatial structure as revealed by microsatellites in plants
Tea			
		<i>Chair: P Hedrick</i>	
16.00 - 16.30	264	Olivieri I & Gouyon P-H	The evolution of migration and other life-history traits: the metapopulation effect
16.30 - 17.00	55	Caballero A & Santiago E	The influence of partial inbreeding on effective population size and fixation rate
17.00 - 17.30	143	Hedrick P	Effective population size of a metapopulation
Wednesday		<i>Chair: RA Nichols</i>	
9.30 - 9.50	54	Byrne K & Nichols RA	The origin and maintenance of London Underground (metro) mosquitoes
9.50 - 10.10	158a	Jaarola M & Tegelstrom H	Colonization history of Fennoscandian field voles (<i>Microtus agrestis</i>) as revealed by mitochondrial DNA
10.10 - 10.30	160	Jager CR	Host related genetic differences between endo-parasitoid populations
10.30 - 10.50	228	Meglecz E, Pecsénye K & Varga Z	Genetic variability in different subspecies of <i>Parnassius mnemosyne</i>
Coffee		<i>Chair: E Arnason</i>	
11.30 - 11.50	297	Reig S	Skull size and shape variation of weasels (<i>Mustela nivalis</i>) from North America
11.50 - 12.10	181	Koh HS	Geographic variation of mtDNA restriction fragments of common rat, <i>Rattus norvegicus</i> Caraco Pallas (Rodentia, Mammalia), from Korea
12.10 - 12.30	225	McMillan WO & Palumbi SR	Demographic information contained within the mtDNA genealogies of recently formed pacific butterflyfishes (Chaetodontidae)
12.30 - 12.50	12	Arnason E, Palsson S & Kristinsson K	Atlantic cod cytochrome B sequence variation: test of two hypotheses on cod genetics
Thursday		<i>Chair: I Olivieri</i>	
9.30 - 9.50	35	Bonnin I, Prosperi J-M & Olivieri I	Genetic markers and quantitative genetic variation in a selfing plant species, <i>Medicago truncatula</i> (Leguminosae): a comparative analysis of population structure
9.50 - 10.10	308	Ronfort J & Couvet D	Selection on selfing rate in structured populations
10.10 - 10.30	323	Schierup MH & Olesen J	Self-incompatibility and a positive correlation between heterozygosity and fitness in <i>Arabidopsis petraea</i>
10.30 - 10.50	6	Alexandersson R	Pollen dispersal within and between natural populations of the non-rewarding orchid <i>Calypso bulbosa</i>
Coffee		<i>Chair: MG Sergeev</i>	
11.30 - 11.50	329	Sergeev MG	Spatial structures of grasshopper populations
11.50 - 12.10	125a	Giles B	From population birth to extinction: small scale metapopulation dynamics in <i>Silene dioica</i>
12.10 - 12.30	157	Ingvarsson PK	The effect of delayed population growth on the genetic differentiation of local populations subject to frequent extinctions and recolonisations
12.30 - 12.50	395	Volodin S	The reproductive isolation mechanism of Black Sea whiting populations

16) Current topics in population structure

Thursday		Chair: JKM Brown	
14.00 - 14.20	24	Beerli P	Maximum likelihood estimation of migration rates in a two-population model using gene trees
14.20 - 14.40	46	Brown JKM & Altham PME	Estimating the frequency of sex in haploids: an approach using computer-intensive statistics
14.40 - 15.00	74	Couvett D	Multigenic estimates of population structure
15.00 - 15.20	118	Gaggiotti OE	Population genetic models of source-sink metapopulations
Tea			
		Chair: JKM Brown	
16.00 - 16.20	124	Gentile G & Sbordoni V	A comparison of private alleles, G_{ST} and θ for quantitative estimates of gene flow levels: <i>Andronisus dentiger</i> as a study case
16.20 - 16.40	257	Nunney L	The effective size of spatially structured populations

Posters

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|------|-------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------|
| 20 | Baranyi C | Genetic and morphological variation in Austrian populations of roach (<i>Rutilus rutilus</i> , Cyprinidae, Teleostei) |
| 50 | Bubli O | Geographic variation of <i>Drosophila melanogaster</i> populations from the former USSR for enzyme loci and quantitative traits |
| 59 | Carmona MJ, Gomez A & Serra M | Habitat conditions as potential factors affecting reproductive isolation among sympatric populations of rotifer |
| 61 | Sbordoni V, Allegrucci G, Caccone A, Cesaroni D, Fortunato C, Venanzetti F & Cataudella S | A multi-technique approach to the study of genetic structure of Mediterranean populations of the sea bass <i>Dicentrarchus labrax</i> |
| 66a | Ciofi C, Bruford M & Swingland R | Population genetics of the Komodo dragon <i>Varanus komodoensis</i> |
| 73 | Cotran EG | Genetic diversity in the horse (<i>Equus caballus</i>) |
| 136 | Guglielmino CR, de Silvestri A & Martinetti M | Isolation by distance is recognised in an Italian province through surnames and HLA genes |
| 147 | Hindar K & Tufto J | Dispersal and gene flow in migratory fish populations |
| 149 | Hogberg N & Stenlid J | Genetic structure of the wood decay fungus <i>Foromitopsis rosea</i> in Sweden and Russia |
| 151a | Holm S & Bengtsson BO | Genetic variation in <i>Potentilla argentea</i> L. (s.l.) in Southern Sweden |
| 208 | Machordom A, Zardoya R, Almodovar A & Bautista JM | RFLP of a mitochondrial DNA fragment in several populations of Spanish brown trout (<i>Salmo trutta</i> L.) |
| 212 | Maleeva J & Kolesnikov AA | The population diversity of <i>Phytophthora infestans</i> in Russia as revealed by PCR-based mtDNA analysis |
| 241 | Montalvo A, Conard SG & Conkle MT | Population structure and clonal variation in <i>Quercus chrysolepis</i> Liebm. (Fagaceae) |
| 242 | Mougel, F & Ferrand N | Population studies of wild rabbit in the Iberian peninsula |
| 252 | Nielsen EEG, Loeschke V & Hansen MM | Genetic structure of European populations of Atlantic salmon (<i>Salmo salar</i> L.) inferred from RFLP analysis of PCR amplified mtDNA |
| 259 | Callejas C & Ochando MD | Use of randomly amplified polymorphic DNA (RAPD) markers for genetic analysis in the genus <i>Barbus</i> |
| 260 | Reyes A & Ochando MD | Isozyme, RAPD and mtDNA differentiation in geographically distant populations of <i>Ceratitis capitata</i> |
| 309 | Knoll S & Rowell-Rahier M | Population structure of an alpine chrysomelid beetle - what scale matters? |
| 364 | Triest L | Genetic diversity and habitat fragmentation of <i>Narcissus</i> |
| 366 | Ulizzi I & Zonta LA | Sex ratio and natural selection in humans: inter- and intrapopulation analyses |
| 383 | van Rossum F, Vekemans X, Gratia E & Lefebvre C | Isozyme variation in relation to ecotypic differentiation and population size in <i>Silene nutans</i> |

17) Hybrid zones

Nick Barton, ICAPB, Univ. of Edinburgh, West Mains Rd., EH9 3JT, UK

Appleton Tower Lecture Theatre 4/5

Wednesday			<i>Chair: N Barton</i>	
9.30 - 9.50	41	Boissinot S, Desmarais E & Boursot P	Selective sweep of Y chromosome and genetic incompatibilities in the house mouse: selfish genes in action?	
9.50 - 10.10	16	Baird SJE	A new interpretation of <i>Mus</i> autosomal marker clines in Denmark	
10.10 - 10.30	13	Auffray J-C & Alibert P	Morphology and selection through the house mouse hybrid zone in Europe	
10.30 - 10.50	91	Mathieu E, Baird SJE, Boursot P & Dod B	Differential selection on X chromosome loci in the hybrid zone between <i>Mus musculus musculus</i> and <i>M. m. domesticus</i>	
Coffee			<i>Chair: N Barton</i>	
11.30 - 11.50	214a	Manolakou K, Dod B, Orth A, Bonhomme F & Boursot P	Genomic interactions and segregation distortion in artificial hybrids of mouse	
11.50 - 12.10	0	Abermethyl K	The establishment of a hybrid zone between red and sika deer in Scotland	
12.10 - 12.30	130	Klepsch L & Gollmann G	A contact zone of three species of crested newts (<i>Triturus cristatus</i> superspecies, Salamandridae)	
W 12.30 - 12.50	48a	Bugter RJF, Arntzen JW & Barton NH	Analysis of the terrestrial habitat component in a <i>Bombina</i> hybrid zone using remote sensing	
Friday			<i>Chair: JM Rubio</i>	*** Move to Lecture Theatre 5 ***
9.30 - 9.50	311	Rubio JM	Speciation through hybrid zones: gene flow, Haldane's Rule and imprinting	
9.50 - 10.10	245	Muller, J & Sturtzbecher C	Genetic and ecological differentiation in a transition zone of two closely related <i>Gammarus fossarum</i> forms	
10.10 - 10.30	62	Chenuil A, Crespin L & Berrebi P	Genetical structure at spawning and non-spawning season in a fish hybrid zone	
10.30 - 10.50	389	Verra F, Cianchi R, Arduino P, Bullini L, Rossi W & Corras B	Natural hybridization between <i>Orchis laxiflora</i> and <i>O. palustris</i> in Italy	
Coffee			<i>Chair: A Porter</i>	
11.30 - 11.50	64	Ungaro A, Arduino P, Cianchi R & Bullini L	Asymmetrical introgression between <i>Papilio machaon</i> and its endemic Sardinian-Corsican relative <i>Papilio hospiton</i> (Lepidoptera, Papilionidae)	
11.50 - 12.10	165	Jiggins C, O McMillan & Mallet J	Genetic and reproductive dynamics of a semispecies hybrid zone in <i>Heliconius</i> butterflies (Nymphalidae: Lepidoptera)	
12.10 - 12.30	26	Benninger P, Porter A & Geiger H	Differences in diapause response across a hybrid zone between <i>Pieris napi napi</i> and <i>P. napi bryoniae</i> (Lepidoptera: Pieridae) at Pont de Naut, Switzerland	
12.30 - 12.50	406	Wenger R, Porter A & Geiger H	The <i>Pieris napi/bryoniae</i> hybrid zone at Pont de Naut, Switzerland: no selective importance of the two host plants <i>Alliaria petiolata</i> and <i>Biscutella laevigata</i>	
Lunch			<i>Chair: J Mallet</i>	
14.00 - 14.20	65	Cianchi R, Mattiveci S, Nascetti G, D'Amelio GS, Paggi L, Arduino P, Orecchia P, Berland B, Bratley J & Bullini L	Introgressive hybridisation between endoparasite ascarid worms <i>Phocascaris phocae</i> Host 1832 and <i>P. cystophorae</i> Berland 1864 (Nematoda, Ascaridoidea)	
14.20 - 14.40	142	Hauser TP, Ostergaard H & Jorgensen RB	Hybridisation ability between populations of weedy <i>Brassica campestris</i> and varieties of oilseed rape (<i>Binapus</i>): fitness of parental, hybrid and back-cross plants	
14.40 - 15.00	171	Katoh M & Ribi G	Genetic variation of sympatric and allopatric populations of hybridizing freshwater snail species	

Posters

17) Hybrid zones

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|------|------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------|
| 109 | Flanagan NS | The existence of an alpine hybrid zone provides further insights into the phylogeography of the meadow grasshopper, <i>Chorthippus parallelus</i> |
| 158 | Jaarola M, Tegelstrom H & Fredga K | A contact zone with non-coincident clines for mitochondrial DNA and Y chromosome markers in the field vole (<i>Microtus agrestis</i>) |
| 190a | Kruuk L | Habitat preference as a barrier to gene flow in hybrid zones |
| 283a | Pialek J & Barton NH | The spread of an advantageous allele across a barrier: effect of deme size and selection against heterozygotes |
| 350 | Summers A | The causes and significance of Haldane's Rule in the meadow grasshopper <i>Chorthippus parallelus</i> |
| 362 | Thulin C-G, Jaarola M, Tegelstrom H & Fredga K | Introgression of mtDNA between two hare species in Scandinavia |
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ABSTRACTS

Abstracts are printed in alphabetical order, by presenter. The numbers of the talk/poster, and the number of the symposium, are given on each abstract. These numbers are also given in the list of delegates, at the end of this book.

The establishment of a hybrid zone between red and sika deer in Scotland

Kate Abernethy *

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* current address; C.I.R.M.F., B.P. 769, Franceville, Gabon.

Sika deer (*Cervus nippon*) were introduced into the range of native scottish red deer (*Cervus elaphus*) in the late 1800's at at least 9 locations where feral populations established. Although the numbers introduced were small; up to a dozen at any one site, a century later they are present in many thousands, on around 35% of Scotland's deer range.

Hybridisation has been reported in many locations, but has been documented in detail in the populations of the Kintyre and Cowal peninsulas in south west Scotland, where hybridisation is extensive. The genetic architecture of this hybrid zone has been described in patterns of nuclear allele frequencies, mitochondrial haplotype frequencies, local heterozygote deficits and linkage disequilibria.

Comparison of the rates of introgression of nuclear and mitochondrial DNA markers indicate how differences in the dispersal distances of males and females influence the structure of the hybrid zone. Inter-sexual differences in ecology can change the selective value of a quantitative trait dependent on the sex of the bearer. The zone is modelled as a "wave of advance" of selected loci and hitch-hiking loci, and the implications for this model of differences in the ecology of the two sexes are discussed.

As well as providing an insight into the establishment of a mammalian hybrid zone, introgression of the red deer genome poses problems for conservation policy in Scotland. The history of sika deer in Scotland provides a case study of the potential impact of releasing exotic mammals into the range of a congener.

Virulence and parasite transmission route:
A protozoan Jekyll and Hyde

Philip Agnew^{1,2} & Jacob Koella²

¹ Experimental Ecology, ETH Zurich, ETH Zentrum NW, CH-8092 Zurich, Switzerland.

² Dept Zoology, University of Århus, Universitetsparken B135, DK-8000 Århus C, Denmark.

The "Strange Case of Dr Jekyll and Mr Hyde" is the fabled tale of the good and evil within an individual. We present results, following evolutionary predictions, of the dual nature of a single parasite's virulence when associated with two transmission routes.

The microsporidian *Edhazardia aedis* is parasitic to the yellow fever mosquito, *Aedes aegypti*. During its life cycle it produces two types of spores. Binucleate spores pass the infection from mothers to offspring (vertical transmission). Uninucleate spores pass the infection between larvae in the aquatic environment (horizontal transmission). Vertical transmission benefits from reduced virulence as this maintains host survival and fecundity. Horizontal transmission benefits from higher virulence as this parasite requires host larval death prior to the release of uninucleate spores into the environment.

Following experimental larval infections we recorded host fitness traits in female mosquitoes that survived to adulthood, relating them to the type and number of microsporidian spores they contained. Fluctuating asymmetry of wings was recorded as an indicator of the developmental stress an individual had experienced. Blood feeding is a key determinant of mosquito fecundity and survival. Blood feeding success was recorded as whether a female would feed when presented with a human arm for four minutes.

Infected females containing binucleate spores for vertical transmission had higher levels of asymmetry and lower blood-feeding success than uninfected controls. The presence of uninucleate spores in adults reflects a failed attempt of horizontal transmission by the parasite. Females with these spores had the highest asymmetry and the lowest blood-feeding success. In addition, neither asymmetry nor blood-feeding success was correlated with the number of vertically transmitting spores. In contrast, as the number of horizontally transmitted spores increased, asymmetry increased and blood-feeding success decreased.

Thus, as evolutionary theory predicts *E. aedis* demonstrates its Jekyll and Hyde nature when pursuing vertical and horizontal transmission routes.

Evolution of lekking behaviour

Rauno V. Alatalo, Dept. of Biology, University of Jyväskylä, P.O.Box 35, FIN-40351 Jyväskylä, Finland.

Leks are aggregations of males that females visit primarily for the purpose of mating. Clumped male sexual display occurs in a wide variety of taxa from birds and mammals to insects. From the male point of view, if the probability of mating is enhanced for the clumped males, it is easy to understand the evolution of lekking. The question why females do mate with aggregated males rather than with single males has turned out to be much more difficult to answer. It is extremely difficult to estimate, under natural conditions, any benefits that females might gain by choosing aggregated males. Thus, one may easily question whether it pays for females to prefer clumped males, or whether females passively end up with mating in male aggregations as a consequence of something more trivial. While the principle of parsimony makes sense in the scientific endeavour, it is hazardous to reject seemingly more complicated explanations involving active female choice just because of the difficulties in testing them. Furthermore, in the few well studied cases there is evidence that females are actively preferring some of the males, and that females prefer clumped males per se. Most importantly, the only study that has been able to address the question whether such choosiness might accrue benefits in terms of the quality of offspring has indeed produced positive evidence in favour of the idea. Also, choosy females may gain immediate fitness benefits, if choosiness enhances female fertility or future survival. A particularly confounding feature of the leks is that frequently male-male interactions play a significant role in male mating success. Thus, it seems that it is the benefits to males, not to females, that need to be considered when explaining the lekking behaviour. However, from the female point of view, mating with the dominant male may be equally good or even more beneficial than mating with the most ornamented males. It is a challenge for the future studies to unravel these questions, but presently it seems that the role of active female choice is far too easily neglected.

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Recent advances in developmental genetics are having a profound impact on the study of comparative anatomy and phylogenetics in vertebrates. By providing alternatives to (and in some respects undermining) established perceptions of homology and morphological evolution, they pave the way for radical re-interpretations of certain longstanding problems. Some of these new interpretations concern structures whose development has not yet been studied in detail; they are untested hypotheses, which raise important further questions about evolution and development. A good example is the interpretation of coelacanth fin structure.

Coelacanth fishes (exemplified by the living *Latimeria*) have anal and posterior dorsal fins with complex branched endoskeletons. In structure (including soft anatomy), these fins correspond precisely to coelacanth paired fins, but differ fundamentally from the segmentally structured dorsal and anal fins of other sarcopterygians. Phylogenetic parsimony indicates that coelacanths are uniquely derived in having paired-fin-like dorsal and anal fins.

Traditional homology criteria stress topographical identity, and thus identify the posterior dorsal and anal fins of coelacanths with those of other sarcopterygians. Their structural similarity to paired fins must then be "explained" as gradualistic convergence driven by natural selection. However, in recent years the study of homeotic mutations has shown that the development of complex structures can under some circumstances be decoupled from their normal sites of expression. This suggests an alternative interpretation of coelacanth dorsal and anal fins as the products of paired-fin developmental pathways which are being expressed homeotically at median-fin sites, in addition to their normal locations.

Unlike the traditional model, this interpretation accounts adequately for the structure and position of the fins. It also carries the startling implication that the transformation from one morphology to another would have been sudden (one organised set of developmental pathways being suppressed in favour of homeotic expression of another set) rather than gradual. However, it is dependent on an at present untested assumption (homeotic transformations can occur between median and paired fin sites even though they are not serial homologues). The new interpretation may potentially illuminate both phylogeny and developmental biology, but it will only do so if used to frame testable developmental hypotheses. This is probably a general rule for the interaction between comparative anatomy, phylogenetics and developmental biology.

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With 2 figures

Summary

Classically the optional 'reproductive' strategy of *L. latrans* has been interpreted as a response to the harshness of the environment (Lewontin, 1965). We regard this 'reproductive' mode by (a) populations with low fecundity and/or low rates of litter development. In one case it is associated with intermediate conditions (Table 1), the document the existence of young feeding on unfertilized eggs as well as the developing siblings inside the mother's reproductive tract. The existence of such cases (Table 1, Cases 1 and 2) of incomplete fertilization of eggs and heterogametic development indicates a deviation from the reproductive pattern suboptimal and to some degree maladaptive. So, whether it is a failure of intraspecific competition among siblings promotes an acceleration of development rates and leads to a situation in which the mother gives birth to an incompletely formed young, or the duration of its stage has been eliminated. An alternative direct developing mode, derived from the preceding one, consists in a drastic reduction of clutch size, more efficient fertilization rates and consequently lack of intrauterine breeding. In this manner, the young is born as a morphologically metamorphosed and not larger than the aquatic larval stage of aquatic populations. We conclude that 'oviparity' and 'optional viviparity' are transitions of which we are currently learning from a process of heterochrony in the mother's reproductive cycle, under the selective pressure associated with intrauterine competition among siblings.

Introduction

Subimantia serranoides is one of 210 species characteristic of an unusual degree of zoogeographic variation in coloration patterns and body proportions. Fricke (1968) recognizes twelve subspecies through the wider ranging distribution of the larva in the Palearctic region. Six subspecies are present in the Iberian Peninsula (Lacort, 1976).

EVOLUTION OF PLANT MITOCHONDRIAL GENOME: MODEL OF A THREE-LEVEL SELECTION PROCESS.

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The plant mitochondrial genome is composed of a set of molecules of various sizes that generate each other through recombination of their repeated sequences (followed by fusion or fission). Molecular observations show that these different molecules are present in an equilibrium state with various proportions of molecules, and different equilibria of molecules have been observed within species. Recombination can produce deleted molecules with a high replication rate but bearing little useful information for the cell (like "petites" mutants in yeast). A previous theoretical study has shown that these incomplete molecules should invade the cell unless there is a replicative advantage to molecules that bear and maintain all of the mitochondrial information. This previous model, however, did not use a hierarchical approach; that is, they considered selection at a single level only (intermolecular). In this study, we use a multi-level model to examine selection among rapidly replicating incomplete molecules and relatively slowly replicating complete, functional molecules. Our model simulates the evolution of mitochondrial information through a three-level selection process including intermolecular, intermitochondrial, and intercellular selection (the intermitochondrial level being facultative). In general, we find that molecules with a high replication rate but incomplete information are at a selective disadvantage (at the mitochondrial and cellular level) relative to complete and functional molecules. The model demonstrates however that the maintenance of mitochondrial information is difficult to explain without the existence of selection at the intermitochondrial level. Our examination of evolutionary equilibria shows that three different equilibria (with different combinations of molecules) can be obtained when recombination rates are lower than a threshold value. This may be interpreted as a drift-mutation balance.

Pollen dispersal within and between natural populations of the non-rewarding orchid *Calypso bulbosa*

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There are few direct measures of pollen dispersal distances within and between natural plant populations. To document patterns of pollen dispersal and to identify maternal plants, I marked individual pollinia with microtags in two populations of the non-rewarding, early-flowering, bumblebee-pollinated orchid *Calypso bulbosa* in two subsequent years. The two populations had about 160 and 200 flowering plants, respectively. Patterns of pollen dispersal varied strongly among years. In the first year, all pollinia deposited in the two study populations had been transferred between plants in the same subpopulation and the median pollen dispersal distance was 4.9 m (range 0.04–56.6 m). In the second year, 35 % of the deposited pollinia had been transported from populations more than 500 m away. Ninety five percent of the marked pollinia retrieved (self-pollinations excluded), had been deposited within the same subpopulation. Most pollinia were deposited less than one day after removal, but in one case the pollinia were deposited ten days after removal. The selfing rate was rather high in the two study population (24 % and 38 % in the first, and 17 % and 1 % in the second year), but may have been inflated by the method used for pollinia tagging. The results show that the level of pollen flow among populations varies considerably among years in *Calypso bulbosa*. In a given year several factors including pollinator competition and local abundance of reward-producing plants are likely to influence patterns of pollen dispersal in this species.

DEVELOPMENTAL STABILITY BEFORE AND AFTER MEIOTIC RECOMBINATION IN SUBSPECIFIC HYBRIDS OF EUROPEAN HOUSE MICE

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Hybrid zones provide valuable models to assess the impact of the two main genetic stresses thought to play an important role on the levels of developmental stability of organisms. In these zones of genetic exchanges, developmental stability should theoretically result from a balance between the stabilising effect of heterozygosity and the disruptive effect caused by breakdown in genomic coadaptation. The predominance of one or the other effect could be used in theory as a measure of selection on hybrid genomes.

The hybrid zone between the two European subspecies of the house mouse (*Mus musculus domesticus* and *M. m. musculus*) crosses Europe from Denmark to Bulgaria. Genetic and parasitological studies performed across this zone of secondary contact all conclude to an apparent genomic incompatibility between these two subspecies. However, we reported in a previous study a global decrease in the levels of fluctuating asymmetry (the most current measure used to assess developmental stability) of lower molar characters towards the centre of the hybrid zone. This suggested that, in hybrid populations, developmental stability may benefit from a heterotic effect while other functions (genetical and parasitological) might suffer from a disruption of genomic coadaptation.

Experimental crosses between the two subspecies were undertaken in the laboratory using randombred strains. This allowed (i) to evaluate the levels of developmental stability before (parental strains and F1) and after (Back crosses and F2) meiotic recombination, (ii) to compare these levels with those found in nature, (iii) to relate developmental stability with fitness traits, and finally (iv) to discuss the relationships between all these features in order to contribute to the understanding of the dynamics the hybrid zone between European house mice.

Sex ratio and sex determination in the dioecious willow species *Salix viminalis*

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Female individuals often outnumber males in willow populations. It has been suggested that the lower fitness of male individuals and male pollen is the cause of these skewed sex ratios. Although the sex determination mechanism has not yet been established for willows, previous studies assume that the deviations will occur after sex has been determined by sex chromosomes.

We found in a genetic study of *Salix viminalis* that the progeny sex ratio can range from extreme female bias to extreme male bias which could not be explained by an environmental cause. Our results also suggest that if sex chromosomes are present in Basket willow, the sex ratio has to be indirectly skewed due to complex systems. On the other hand, we found a simple autosomal sex determination model which may explain the wide range of skewed sex ratios in our study.

R B ANGUS. The use of chromosomes to elucidate recent biogeography and speciation patterns in water beetles (Coleoptera). Good quality preparations of mitotic chromosomes are obtained from eggs (Hydrophiloidea) and from mid gut, testis and ovary of adult beetles, following colchicine treatment, cell inflation by hypotonic potassium chloride, fixation and air-drying. The preparations may be C-banded, and nucleolus organisers may be stained by ammoniacal silver nitrate. G-banding has been demonstrated by *in vitro* treatment of embryos with 5-fluorouridine, but is of limited use.

Species of *Helophorus* often show clear interspecific differences in chromosomal arrangement, which has in some cases revealed species-complexes with clear distributional patterns. There are also chromosome polymorphisms involving inversions, interperated heterochromatic segments, and the presence of B-chromosomes. In the hydrophilid genus *Enochrus* one instance of possible interspecific hybridisation has been found.

Parthenogenesis has been shown in two hydrophiloids, *Anacaena lutescens* Steph. and *Helophorus brevipalpis* Bed. Some Spanish populations of *H. brevipalpis* include a high proportion of triploid females as well as small numbers of males and diploid females. These populations may be the source of females-only populations in Utah, USA. Parthenogenetic material of *A. lutescens*, originally suspected because of an apparent absence of males, differ from bisexual populations in the loss of a small section of one autosome - and are always heterozygotic for this character. Two populations, from Holland and England, include a proportion of triploid specimens, but the chromosomes of the triploids differ between the populations, indicating that triploidy has originated more than once, after the onset of parthenogenesis.

Whereas Hydrophiloidea normally have 18-22 chromosomes, the Dytiscidae generally have many more, with diploid numbers up to 60. Nevertheless, it is often possible to obtain good preparations. Using preparations from mid gut and testis, it has been found that *Stictotarsus griseostriatus* DeGeer is a complex including at least three species. *S. griseostriatus*, from the Baltic coast of Sweden, has 30 pairs of autosomes plus sex chromosomes which are X0 (male), XX (female). *S. multilineatus* Falkenstrom from inland Sweden and Scotland has 28 pairs of autosomes plus X0 sex chromosomes, while populations from the Alps have 27 pairs of autosomes, with the smallest pair apparently fused with one of the long pairs. The third species, from central Spain and the Alpes Maritimes (France/Italy) has 26-26 pairs of autosomes, with a fusion/fission polymorphism which can also be seen at meiosis. Material from both areas includes specimens which are homozygous fused, homozygous unfused, and heterozygous. The X-chromosome of this species is smaller than those of *S. griseostriatus* and *multilineatus*.

Although these results highlight chromosomal complexity and species fragmentation, in most cases species show chromosome stability over wide areas.

P-sequences in *Drosophila*: where did they come from and where are they going?

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P elements seem to be widespread in the genus *Drosophila*. Moreover they have been found in the genus *Scaptomyza* and in species outside of the *Drosophilidae* family, such as *Lucilia cuprina*. Thus P elements are very old components of *Diptera* genome. However, using Southern blot hybridizations, P-sequences have not been detected in those species most closely related to *Drosophila melanogaster*. These contradictory results incite us to research P-sequences in the so-called empty species using the PCR procedure. Oligonucleotide primers have been chosen in the nucleotide sequence of *Scaptomyza pallida* corresponding to highly conserved domains of the P element putative proteins from *D. melanogaster* (or *D. willistoni*), *D. guanche*, *D. bifasciata*, *D. subobscura* and *S. pallida*. From each following species belonging to the *montium* sub-group: *D. davidi*, *D. kikkawai* and *D. tsacasi*, a sequence has been amplified presenting more than 62% of similarity at the DNA level and more than 2% at the protein level with the corresponding region of P element from *D. melanogaster*. By Southern blot analysis, this sequence corresponds to a single sequence; moreover, it allows us to detect in the species where it comes from, P repeated sequences, but much more divergent from *D. melanogaster* P element. Speculations about the origin of this single sequence will be proposed.

Using sequences amplified from the *montium* species as probe, we have detected ancient repeated P sequences in the genome of several true M strains of *D. melanogaster* (empty of any P element), corresponding to an old P family called "archéo-P". This finding reveals the possibility of coexistence of two families of P elements in the *D. melanogaster* genome. We are analysing the "archéo-P" elements in regard to their sequence, structure, number, localisation and the relationship of this family to the modern P element in *D. melanogaster*.

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PROPORTION AMONG BISEXUALLY-REPRODUCING INDIVIDUALS IN POPULATIONS OF MONOGONONT ROTIFERS: A THEORETICAL APPROACH.

Monogonont rotifers are cyclical parthenogens whose populations show bisexual reproduction frequently restricted to some periods of the growth cycle. Bisexual reproduction starts with the production of mictic females, which produce meiotic eggs. If a mictic female becomes fertilized, her eggs develop into diploid resting eggs, the only bisexually-produced eggs, but if she remains unfertilized, her eggs develop into haploid males. Moreover, mictic females can be only fertilized during their earlier ages, before maturation. Therefore, the threshold age at which a mictic female could not be further fertilized affects the fate of that female; the longer that age, the larger the probability of becoming fertilized. On the other hand, that fate is also affected by the male density through male-female encounter probability, and thus by the density of mature, non-fertilized mictic females.

We have modeled this complex looped dynamics in order to address the effect of the maximum age for fertilization on the proportion of the different types of individuals. Moreover, we have studied the consequences of that age on the production of resting eggs, which is an important component of long-term fitness. These consequences allow us to get insights into the evolution of the maximum age for fertilization.

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The Atlantic Cod (*Gadus morhua*) is a wide-ranging high-fecundity wild species which inspite of heavy fishin pressure and the vagaries of the environment continuously supports a large profitable commercial fishery. I recent times the annual catch is one to three million metric tons and the cod fishery has been important fo centuries. How has natural selection equipped cod to support such a fishery — what is the genetic structur of cod populations or what game against nature [2] does cod play?

Two diametrically opposite hypothesis have been put forth on cod genetics: **The Local Stock Concep** of fisheries biology and **The Cod-Starfish Model** of sisyphian genotypes winning the sweepstakes in a environmental lottery [7]. The two hypothesis make different predictions regarding the patterns of variatio in relation to geography *vs.* age-structure.

The local stock concept is based on a concept of a triangle of cod migration: from (1) spawning ground developing eggs and larvae drift with ocean currents to (2) nursery areas where juveniles grow up and recruit t (3) adult feeding grounds whence they make yearly runs for the spawning grounds. Populations are considered mostly reproductively isolate from other such intraspecific populations (a population structure with severely reduced gene flow)—a concept of local adaptation [4]. The concept predicts that neutral mutants show geographical pattern of variation possibly with with local genotypes characterising stocks. Neutral variatio should not show age-class variation.

The cod-starfish model accounts for phenotypic differentiation by postulating intense selection in every generation as part of ecological dynamics in unpredictable environments. Cod with fecundity in million of eggs could play such a game [7]. Under this model neutral variation should not be geographically localized but could show temporal or age-class differences.

In this study samples of over five hundred cod of different ages from fry to adults and sampling localities from Greenland to the Baltic, from the White and the Barents Seas to Norway and Iceland have been subjected to polymerase chain reaction amplification and direct sequencing of a part of the mitochondrial cytochrome *b* gene. A large number alleles, some at polymorphic frequencies, contribute to variation that passes neutral tests (Ewens-Watterson, Ewens exact, Tajima's *D* [1, 6, 3, 5]). Having established neutrality of markers they become useful for tests of the above hypothesis of spatially localised *vs.* temporal variation. Changes in neutral variance between age-classes may indicate variance in total fitness.

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Morphology and selection through the house mouse hybrid zone in Europe

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The dynamics of the hybrid zone between the two European subspecies of the house mouse, *Mus musculus musculus* and *M. m. domesticus* (see Boursot et al., 1993; Sage et al., 1993 for review) has been investigated through several transects for different markers suggesting that selection on sex chromosomes is stronger than that on other markers. The greater susceptibility of hybrid populations to intestinal worms (Sage et al., 1986; Moulia et al., 1993) has been explained by the disruption of co-adapted gene systems related to immunological response in hybrids (Moulia et al., 1991). Additionally, a recent study on fluctuating asymmetry in natural hybrid populations has shown that developmental stability increases in the centre of the hybrid zone (Alibert et al., 1994) underlying that hybrids may benefit of heterotic effects for certain characters, at least for tooth development.

This study provides the first application of the relative warps analysis (Bookstein, 1991, Rohlf, 1993) on natural populations in a hybrid zone (N=269, 18 populations). The aim was to evaluate the within population variability and to establish the pattern of skull shape changes across the hybrid zone. Fluctuating asymmetry on skull was also estimated by the Procrustes method (Bookstein, 1991; Auffray et al., in press).

1) It is shown that the phenotypical variability within populations is not related to the introgression index estimated by the percentage of *domesticus* diagnostic alleles.

2) The plot of relative warp scores against the introgression level presents a logistic-like shape. This suggests that the gene systems involved in the developmental process of skull formation are perturbed or linked to another gene system which is under selection, at least more so than allozymes.

3) The decreasing fluctuating asymmetry in hybrids suggests a higher developmental stability in this group and thus that hybrids may also benefit of a heterotic effect for skull development.

These results lead us to hypothesize that:

1) If skull phenotype is not under selection but linked to another gene system which is, the heterosis on skull development suggests that all biological functions are not disrupted in terms of coadaptation (see also Alibert et al., 1994).

2) If the hybrid skull phenotype is counter-selected, the selection may be related to preferential intrasubspecific mating choice which would not interfere with heterosis of skull development.

Hox genes and the diversification of insect-crustacean body plans

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Crustaceans and insects share a common origin of segmentation, but the specialization of trunk segments appears to have arisen independently in insects and various crustacean subgroups. Such macroevolutionary changes in body architecture may be investigated by comparative studies of conserved genetic markers. The Hox genes are well suited for this purpose: they determine positional identity along the body axis in a wide range of animals. We have examined the expression of four Hox genes in the branchiopod crustacean *Artemia franciscana*, and compared this with Hox expression patterns from insects. In *Artemia* the three 'trunk' genes *Antp*, *Ubx* and *abdA* are expressed in largely overlapping domains in the uniform thoracic region, whereas in insects these genes specify distinct segment types within the thorax and abdomen. Our comparisons suggest a multi-step process for the diversification of these Hox gene functions, involving early differences in tissue specificity and the later acquisition of a role in defining segmental differences within the trunk. We propose that the branchiopod thorax may be homologous to the entire pre-genital (thoracic and abdominal) region of the insect trunk.

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Geographic Variation in Phenotypic Plasticity of Wing Area and its Cellular Basis in *Drosophila melanogaster*

We examined twenty *Drosophila melanogaster* populations collected from a 2600 km north-south transect in the eastern coast of Australia. In laboratory culture at standard larval density and a constant temperature of 16.5°C, genetic clines in wing area, cell size and cell number were found, with all traits increasing with latitude. The cline in wing area was primarily determined by variation in cell number. The pattern of phenotypic plasticity with temperature was investigated in six populations from the transect. Flies were reared at standard larval density and constant temperatures of 14°, 18°, 21°, 25° and 29°C. Wing area showed strong plasticity with temperature. There were also differences among populations in the level and steepness of the response, both increasing with latitude. The plasticity was determined by changes in cell size, but the variation in the level of response was mostly attributable to differences in cell number. We discuss our results in the context of selection processes operating in natural and experimental populations.

5 Tandemly repeated satellite-DNA of Dolichopoda schiavazzii: A test for models on the evolution of highly repetitive DNA

T 2

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Three specific satellite-DNA families can be detected in the genome of the cave cricket *Dolichopoda schiavazzii*. The *pDoP102* and the *pDsPv400* families are species specific for *D. schiavazzii*; the *pDoP500* family is probably present in all *Dolichopoda* species. The three satellite-DNA families were characterized from individuals of three isolated populations with respect to nucleotide sequence, sequence complexity, sequence variability and copy number. So far, our knowledge on the mode of evolution of non-coding, tandemly arranged satellite-DNA is strongly influenced by the conclusions drawn from computer simulations. The unique data set on satellite-DNAs of *D. schiavazzii* seems to allow to test the significance of such theoretical approaches.

At least for *D. schiavazzii* two clear correlations were observed for (i) sequence variability and copy number and (ii) for the repeat length and copy number. The first one is in good agreement with the theory but the second one is not. Thus, a revision of the models have to be proposed.

A New Interpretation of *Mus* Autosomal Marker Clines in Denmark

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It is not clear how we should take cline transects through field areas which have no obvious environmental or geographic restrictions on gene flow. In the first rigorous analysis of the Denmark *Mus* hybrid zone Hunt and Selander recognised this problem, and chose linear transects in the direction of maximum change in overall hybrid index. Since then data on many more autosomal markers has been collected, and likelihood analysis has been recognised as a powerful approach for comparing observations to complex theories. With this in mind a likelihood analysis has been designed to find suitable transects through open field areas. Based upon the same principals as Hunt and Selander's decision process, it gives results consistent to theirs in the context of their study. However, because the approach uses more of the information available from the field samples it reveals more about the structure of the frontier between the two taxa. Using this approach on the larger datasets of allozymic markers now available we gain much better resolution of the geography of the hybrid zone, allowing a clearer interpretation of the clines we observe, and absolute rather than comparative measures of cline width. The analysis provides a framework for an informative synthesis of clines in autosomal markers, sex chromosome markers and quantitative traits in the *Mus* system, thus allowing investigation into the relative selective forces acting upon a variety of genetic components.

SOME TENDENCIES IN THE EVOLUTION OF ENZYMES IN PLANTS

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The evolution of biological catalysis involves structural and functional aspects. Typical for the enzymes as biocatalyzers is that all of them are proteins. The structural evolution consist of structural changes in the enzyme proteins, mainly genetically determined. The evolution of the catalytic function is somehow faster and more detailed. It depends not only on changes in the basic structure of the enzyme molecule, but also on a different mechanism of regulation of the enzyme function, including the feed back regulation influence of low molecular effectors etc. The comparative study on peroxidase and superoxide dismutase in plants related to activity, heterogeneity, the sensitivity and dependence of function on external factors as UV and visible light, high temperature shows several peculiarities of evolution. They may be marked as follows: the SOD function is realized by proteins, containing Fe, Mn or Cu/Zn in the active site, the role of these three forms in realizing the total function changes in the course of evolution, the Cu/Zn form being dominant in higher plants. These forms namely are very stable toward increased temperatures, thus ensuring the enzyme function at extreme situations.

- For the two enzymes an increase of heterogeneity is attained in the course of evolution. The individual isoforms loses individual specificity in the realization of the catalytic function, which is very important for a better adaptation and effective regulation of the catalytic activity.

- In the course of evolution the role of some metabolic effectors, including metal ions, is increased. This is very important for the reaction of enzyme systems to changes in the external factors and the stability in stress situations.

Endocytobiosis in cockroaches and termites: a phylogenetic approach

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The evolutionary history of cockroaches and termites has been debated since the beginning of this century. The termite *Mastotermes darwiniensis* and the wood-eating subsocial cockroaches belonging to the genus *Cryptocercus* are considered to be keys to understanding this issue. Only *M. darwiniensis* among termites and *Cryptocercus* among cockroaches show a double symbiosis (with the wood-digesting protista of the gut and with the bacteriocyte endosymbionts of the fat body), and both have been regarded as survivors resembling the common ancestor of cockroaches and termites. However, cladistic analysis on morphological characters suggests a recent origin of the phyletic line leading to *Cryptocercus* from an existing cockroach family, the Polyphagidae. Moreover, the praying mantids, which do not show either of these symbiotic associations, are regarded by some authors as the sister group of cockroaches. The hypothesis that the double symbiosis of *Cryptocercus* and *Mastotermes* is an ancestral condition would therefore imply repeated losses of symbionts over various lineages. As regards intracellular symbiosis, molecular-taxonomic analysis (16S rDNA sequence analysis) places the bacteriocyte endosymbionts of both cockroaches and *M. darwiniensis* into the same subgroup of the flavobacteria-bacteroides. These studies, while indicating that the endosymbiont of *M. darwiniensis* is a sister group to the endosymbionts of cockroaches, do not show any particular relationship between the endosymbiont of *Cryptocercus* and those of the Polyphagidae. Therefore, in contrast to the results of cladistic analyses on the hosts' morphology, molecular phylogenetic analysis of the endosymbionts agrees with the classic scenario on the evolution of cockroaches and termites.

The bacterial endosymbiont of a mycorrhizal fungus belongs to the RNA group II of Pseudomonads

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Almost 80% land plants are colonized by arbuscular mycorrhizal fungi (AMF) (Bonfante & Perotto 1995, New Phytol. 130, 3-21). Evidence has recently been obtained for the antiquity of this symbiotic association, and it is believed that AMFs have been instrumental in the colonization of land by vascular plants (Simon et al. 1993, Nature 363, 67-69). An intriguing attribute of these symbiotic fungi is their association with some further symbionts, bacteria called Bacteria-Like Organisms (BLOs) which have been observed in the cytoplasm of all examined AMFs. The identification of the BLOs has until now been hampered by the inability to grow them on cell-free media, and no data are available on their phylogenetic position. A useful approach for the identification of uncultured bacteria and for the investigation of their phylogeny is the analysis of the genes encoding for the small subunit ribosomal RNA (16S rDNA).

Intracytoplasmic bacteria-like organisms (BLOs) were detected ultrastructurally in the AM fungus *Gigaspora margarita* in all phases of its life cycle (spores, symbiotic mycelia). 16S rDNA sequence data were obtained for the BLOs of *G. margarita*, starting from spores of this fungus. The obtained sequence was compared with sequences available for representatives of the various eubacterial lineages. Molecular phylogenetic analysis unambiguously placed the endosymbiont of *G. margarita* into the rRNA group II pseudomonads (new genus *Burkholderia*). To prove that the obtained sequence derived from the BLOs, polymerase chain reaction (PCR) assays were set up by using specifically designed oligonucleotides. In addition, morphological observations by using fluorescent probes (LIVE/DEAD BacLight bacteria Viability Kit) revealed a high number of vital bacteria inside the spores of *G. margarita*. In conclusion, the experiments opened interesting questions on the roles of these bacterial endosymbionts in AM symbiosis.

GENETIC AND MORPHOLOGICAL VARIATION IN AUSTRIAN POPULATIONS OF ROACH (*Rutilus rutilus*, Cyprini lae, Teleostei)

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Five samples of Roach were taken from the Austrian section of the Danube, from geographically close sites which differ in their connectedness to the mainstream. Two more samples were taken from River Drau and the subalpine lake Wallersee. Enzyme polymorphism of 14 loci was analysed and mean heterozygosity was used as a measure of genetic variation. Results show only minimal genetic differences between the samples from the river Danube. To characterise samples morphologically, conventional characters as well as truss characters were measured at each of the 230 investigated individuals. Morphological variation could be described by five Principal Component Axes which were calculated from the correlation matrix. The determinant of the variance-covariance matrix was taken as a measure of morphological variance and the level of morphological integration was calculated from the determinant of the correlation matrix following Cheverud et al (1983). Genetic and morphological variation were not correlated, but there was a significant correlation between morphological integration and variation which indicates that samples with highly integrated morphological information were the less variable ones.

21. We present a quantitative model of mutation and selection that allows for the coexistence of multiple alleles at a locus with very small differences between alleles. The determination of fitness depends on many loci. Previous attempts to construct similar models have typically assumed that all mutations produce a decrease in fitness, and this has led to a tendency for the average fitness of population members to decline when population numbers are finite. In this model we incorporate some of the ideas of R.A. Fisher, so that both deleterious and beneficial mutations are possible. As a result, the population approaches a stationary distribution. We have shown in work presented elsewhere that, under the assumptions of this model, sex and recombination can have large positive effects on fitness when the selective effects of the various alleles within the genome combine in a multiplicative fashion. However, this typically results in a large genetic load, which may be biologically unrealistic.

Here we examine the effects of synergistic epistasis. Roughly speaking, this regime leads to a situation where the effects of a deleterious mutation are more harmful when an individual already has a high load of deleterious mutations than when the individual's genome is of relatively good quality. The strength of this effect can be tuned through a parameter called α . As α increases, the degree of synergistic epistasis also increases.

We show that it is possible to choose values of α so that genetic load is much smaller than in the multiplicative model, but obligate sexual reproduction is still favoured over all alternatives. Furthermore, the value of α has a very strong effect on the consequences of a transition from sexuality to asexuality. In particular, when α is large (i.e., strong synergistic epistasis) a sexual population that becomes asexual will undergo a much more rapid decay of fitness than in the case where α is small. Thus, epistasis can determine whether the advantages of sex occur over the long term or the short term.

CLASSIC GENETIC MODELS IN COEVOLUTION

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In recent years there has been an increasing recognition that the coevolutionary genetics of host-parasite systems cannot be separated from their ecology. Yet much of the discussion about the genetics of coevolution still centres around a few "classic" models. This paper will present a constructively critical review of a sample of these models. The approach taken will be to examine the assumptions, both implicit and explicit, of the models and the generality of their results.

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EXPLAINING HIGHER PLANT RADIATIONS: DO RADICAL DEVELOPMENTAL MUTATIONS DRIVE PHYLOGENETIC CHANGE ACROSS FITNESS SEASCAPES?

What is an evolutionary radiation? Within a specified clade and a specified period of time, a radiation is best defined as an exceptionally high surplus of species natality (speciation) over species mortality (extinction) and of character acquisition over character loss within the overall pool of species.

Why is a phylogenetic context so important in the study of radiations? A cladogram tests by congruence initial assertions of character homology, preventing confusion of phenotypically similar but genotypically dissimilar characters; it also simplifies the study of character change by discounting plesiomorphies. The explicit sequence of acquisition (or loss) of sets of character states on each cladistic branch provides biologically meaningful phylogenetic correlations of dynamic character-state *transitions*, rather than biologically meaningless statistical correlations of static character states. It also permits historical measurement of phylogenetic constraints on the character diversity and degree of divergence (disparity) of lineages, rather than ahistorical measurement of unconstrained phenetic similarity.

Are evolutionary radiations tracked more accurately by morphological or molecular data? Changes in genotype at the level of nucleic acid sequences are more clock-like than changes in phenotype. Moreover, in most ecological settings natural selection of phenotypes is stabilising rather than directional, promoting stasis rather than change (punctuated equilibrium). Most radiations occur when (1) a key innovation allows primary invasion of a formerly unoccupied habitat type, (2) a key innovation allows finer niche partitioning within an already occupied habitat type, or (3) an environmental catastrophe severely creates temporarily vacant niches in a specific habitat, allowing secondary invasion. This emphasis of niche occupation and saturation predicts rapid initial radiations followed by relative stasis. Such evolutionary patterns will on average be tracked more effectively by morphology, which directly reflects evolutionary tempo, than molecules, which blindly accumulate largely unexpressed point mutations.

Which genes underpin evolutionary radiations? If radiations truly require key innovations and/or low-competition environments and lead to greatly increased phenotypic diversity, radical change reflecting mutation in key developmental genes provides the most rapid credible underlying mechanism. Adaptive radiations based on classic Hardy-Weinberg equilibria within infinite panmictic populations constitute the reddest of herrings if selection pressure is low, adaptation of secondary importance and speciation occurs across a single generation (saltation) or very few generations (parasaltation) of mutant 'hopeful monsters'.

Should adaptive landscapes be replaced with fitness seascapes? Sewall Wright introduced the powerful analogy of adaptive landscapes to explain his parasaltational 'shifting balance' theory. This paradigm allowed *ad hoc* factors in small populations to overwhelm selection and thus transgress fitness depressions separating local fitness optima, potentially giving the population a new lease of evolutionary life. However, a *lethally* low fitness depression cannot be crossed via a series of progressively changing generations ('swimming') – this requires a single high-risk evolutionary event via radical mutation ('flying'). On a fitness *landscape* the newly targeted peak is likely to be already occupied and therefore unoccupiable, particularly given that estimates of raw fitness generally overlook the great importance (especially among sessile plants incapable of direct competition) of home-field advantage: one species can resist invasion by another species of higher intrinsic fitness simply by occupying the contested niche first. But replace the concept of a static fitness landscape with a dynamic fitness *seascape*, constantly changing in response to environmental fluctuations, and theoretical peaks become too unstable to be occupied by populations indulging in the painfully slow upward progress dictated by natural selection; the optimal niche therefore remains available for any hopeful monster fortuitously possessing the appropriate characters.

Maximum likelihood estimation of migration rates in a two-population model using gene trees

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T16

Estimation of different population parameters (e.g. effective population size, migration rate) are crucial for studies in ecology and conservation biology. The current progress in molecular techniques allows the usage of methods for the estimation of these parameters which can take into account the topology of a genealogy and therefore the sequence of mutation. In a two-population model a maximum likelihood approach is used to estimate jointly the two effective population sizes and the two migration rates. The methods uses coalescence theory expanded to include migration events. The likelihood is the sum over all possible genealogies of the product of the probability of the genealogy given the data and the mutation rate per locus per generation, and the probability of the genealogy given the effective population sizes and the migration rates: most summands of this sum do not contribute very much to the final result. The sum is only influenced by genealogies with high likelihoods, so only those need to be considered. This is achieved by a Markov chain Monte Carlo approach, in which a new genealogy is created by a small random arrangement of the old genealogy and accepted if the ratio of the new and the old likelihood is bigger than a randomly drawn ratio ("importance" sampling). Finally the parameter estimates per locus are combined using a Gamma prior for the mutation rate. The resulting parameter estimates are considered better estimates than those with the traditional F_{ST} approach or the s approach of Slatkin and Maddison, because the estimation process does not assume a true genealogy like the other methods. In near future the program will be available for free on our www-server <http://evolution.genetics.washington.edu/lamarc.html>.

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Comparative biology of life cycles in seaweeds

The brown seaweeds (phylum Phaeophyta) are structurally and ecologically rather uniform, but vary enormously in sexual development. Some forms have an isomorphic alternation of haploid and diploid plants; in others the haploid generation is partly or completely suppressed. The gametes may be morphologically uniform, or may be differentiated to some extent as male and female. Parthenogenetic or vegetative repetition of parts of the life cycle often occurs. Moreover, these asexual processes may be associated with the alternation of morphologically different phases. The diversity of growth, sex and gender in the group will be used to test current theories of the life cycle.

DIFFERENCES IN DIAPAUSE RESPONSE ACROSS A HYBRID ZONE BETWEEN *PIERIS NAPI*
NAPI AND *P. NAPI BRYONIAE* (LEPIDOPTERA: PIERIDAE) AT PONT DE NANT,
SWITZERLAND

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T17

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Pieris napi napi is widespread at low elevations in Europe and *Pieris napi bryoniae* is endemic to the Alps; they are reported to hybridize at elevations of approximately 1000m. At 400m, *P. napi napi* flies in 3-4 generations annually, whereas *P. napi bryoniae* only has one generation above 1200m. This difference could be due to environments of different predictability: the higher the elevation, the more severe and unstable the climate. Severe conditions allow only one generation per year in the maximum, whereas the milder the conditions are the more generations are possible. This suggests that, first, populations from low elevations should develop an assemblage of genes allowing them to produce as many generations as possible, and second, the variance in the timing of diapause termination should increase with elevation because this way the mortality risk of severe conditions can be spread.

In a 14km long transect with a difference of elevation of 1500m several females were caught and their offspring were reared in a diapause-inducing regime of 8°C and 6L/18D photoperiod. After the pupae were kept for 3 months in the refrigerator at 4°C and 6L/18D, members of 10 different families were transferred to 20°C and 18L/6D. The days until eclosion were counted and the data analysed.

P. napi bryoniae hatched significantly later than *P. napi napi*. This suggests that *P. napi napi* developed indeed a different assemblage of genes determining its diapause response. There also was a correlation between the elevation that females were captured and the variance of the hatching period of their offspring. Both results agree with predictions from life-history theory.

Using mitochondrial DNA to examine the Pleistocene history of *Podisma pedestris*

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Large scale and long term climatic changes affect species ranges. The current genetic substructuring of a species is partly a consequence of past population distributions. Understanding the way species, or groups of species, were distributed over the ice ages and particularly their more recent movements could help to understand their present day genetic composition and make predictions concerning human induced changes. *Podisma pedestris* is a representative of species with arctic alpine distributions. The mtDNA (more specifically a 310bp section of the CO1 region) of individuals, collected from populations across the species range, is being sequenced in order to obtain a molecular phylogeny from which the history of *Podisma's* distribution may be inferred. Preliminary results will be discussed.

Competition between pure and mixed strategists in evolutionary games

Bergstrom CT, Godfrey-Smith P & Lachmann M

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Many ecological and evolutionary models predict variation in behavior when a population is at equilibrium. This variation can be in the form of a polymorphic population of pure strategists or a monomorphic population of mixed strategists. While static ESS models are very useful in predicting the existence of variability, they do not readily distinguish between the alternative realizations of variability: pure strategist polymorphisms and mixed strategist monomorphisms. Here, I address this distinction by means of stochastic, finite population models. In the games considered, natural selection often favors mixed strategists. The selection pressures behind these results are explored, with a particular focus on their operation in the hawk-dove game.

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A common feature of insects is the subdivision of the body in homologous segments. Two classes of genes have been shown to establish metamerie in *Drosophila*. Segmentation genes establish the basis of segmentation, and a set of homeotic genes determines the identity of each metameric unit (Nüsslein-Vollhard et al., 1982).

In the honeybee *Apis mellifera* seven homeobox containing genes have been cloned with high homologies to their corresponding putative *Drosophila* homologues. But until today nothing is known about the structural organization of homeotic genes in the honeybee genome (Walldorf et al., 1989).

Scr (*Sex combs reduced*), *Dfd* (*Deformed*) and *Antp* (*Antennapedia*) from *Apis* were hybridized *in situ* (Beye and Moritz, 1993) to interphasenuclei and to metaphase chromosomes. We found the three genes clustering at the same chromosome region. The signals in the interphasenucleus occurred together at the same position indicating a distance smaller than 850 kb between these loci.

The three insects *Drosophila*, *Tribolium* and *Apis* studied so far show a highly conserved structural organization of the homologues homeotic genes.

In *Drosophila* the three genes studied here are clustered in the ANT-Complex, but other homeotic genes cluster in the BX-Complex (Gehring and Hiromi, 1986). This contrasts sharply to the beetle *Tribolium* showing only one single HOM-Complex (Beemann, 1987). Further experiments on the structure of homeotic genes in *Apis mellifera* may indicate the evolutionary older organization type in insects.

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Variation in reproductive success of the anther smut fungus *Ustilago violacea* on two related host species, *Silene alba* and *S. dioica*.

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The relative success of a plant pathogen is determined both by its "virulence" (the range of host genotypes that it can successfully infect), its "aggressiveness" (the reproductive success on a given host) and its transmissibility. One aspect of aggressiveness is the alteration of host traits by the pathogen in such a way that it increases components of the pathogen's reproductive success ("host manipulation"). The anther smut fungus *Ustilago violacea* (*Microbotryum violaceum*) is a systemic, host-sterilizing pathogen of plant species in the pink family (Caryophyllaceae). The fungus produces its spores in the anthers of infected hosts, and is transmitted by insects that are both pollinators and vectors of the disease. The fungus induces infected plants to produce more flowers, thus increasing the number of "spore production sites".

We investigate whether strains from two related host species, *Silene alba* and *S. dioica*, differ in (1) infectivity, (2) the ability to manipulate flower production, (3) spore production per infected flower, and (4) floral traits that may affect attractiveness to vectors and hence transmissibility on the two host species. We specifically ask whether the reproductive success of strains is traded off between host species and whether components of reproductive success of strains highest on the host species from which they originate (host adaptation). The results indicate that there is trade-off in the reproductive success of strains on male hosts of the two host species due to a combination of host-pathogen interactions of different components of reproduction. On *S. alba*, native strains have a higher reproductive success because of a higher virulence and higher spore production per flower. On *S. dioica*, native strains outperform non-native strains because of a higher ability to increase the number of flowers per plant in which spores are produced.

Gamete Recognition and Molecular Variation in Circumarctic Sea Urchins (Echinoida: Strongylocentrotidae)

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Sympatric marine free-spawners have to rely on molecular interactions of their gamete surfaces for mate recognition. In echinoid echinoderms, a sperm protein, bindin, has been characterized as being responsible for the species specificity of fertilization. Parts of the bindin gene were sequenced in the widespread, closely related sea urchin species *Strongylocentrotus droebachiensis* and *S. pallidus*. They occur sympatrically throughout northern high latitudes; their depth distributions and spawning seasons overlap. They may hybridize asymmetrically and their morphological distinction is sometimes ambiguous.

Partly through length mutations and intragenic recombination, the bindin sequence evolves rapidly within and between species, especially in a region of short amino acid repeats. *S. pallidus*, a deep-water species, is highly polymorphic and has distinct groups of bindin alleles. *S. droebachiensis*-populations may have been less stable due to disease and pleistocene sea level changes, and are genetically more uniform around North America but differ between the Western and Eastern Atlantic Ocean.

In vitro fertilization assays show that at least one other recognition step, the induction of the acrosome reaction by egg jelly, is involved in gametic reproductive isolation between the two species. The two barriers are of unequal importance between different species within the same genus.

Endocytobiosis in cockroaches and termites: a morphological approach P142

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It is well known that the endocytobiont flavobacteria of the Blattaria are integrated in a cellular structure (the bacteriocyte) with which they enter into a morpho-functional relationship: this can be shown by particular systems of membranes which involve the bacterial envelopes and the symbiont-bearing vacuole. We studied this relationship between the prokaryote and the bacteriocyte in three Blattaria families (Blaberidae, Blattellidae and Cryptocercidae). The symbiotic population is assured to offspring transovarially and is thus integrated in the ontogenetic processes. We were able to identify two models represented by *Blattella germanica* (Blattellidae) and *Periplaneta americana* (Blattidae) in which there are different relationships linking the symbionts to the vitellophages in the early phases of embryonic development. The *P. americana* model is particularly interesting, with the formation of a complex intradeutoplasmic symbiotic structure ("primary mycetome"); its morpho-functional significance will be discussed. In the following phases of development there is a progressive regression of this structure and the bacterial population within it abandons the yolk sac and moves to the epineural sinus. At this point the symbionts are phagocytosed by the embryonic plasmatocytes which then become bacteriocytes. The formation of these cells therefore follows an analogous pattern to that observed for *B. germanica*, which suggests that the bacteriocyte formation took place within the order Blattaria, following substantially similar coadaptive processes which have involved both the host cell and the symbiont prokaryote. As well as in the Mastotermitidae, which present a similar symbiotic situation to the Blattaria, we have been able to observe the presence of bacteria within the trophocyte cytoplasm and/or nucleus in two other families of termites. These bacteria are however assigned to the proteobacteria.

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The dominant theories for the evolution of ageing are antagonistic pleiotropy and mutation accumulation. Both imply the evolution of increasing intrinsic mortality rates and decreasing fecundity rates as organisms age. In turn, such patterns are used to infer the existence of senescence in both natural and laboratory populations. Medawar showed that a decrease in lifespan is not necessarily associated with senescent mortality. Following Medawar, senescence has often been inferred from an age-dependent increase in the mortality rate due to intrinsic, physiological causes. However, this criterion is not sufficient to diagnose senescence. When there are physiological tradeoffs between reproduction and mortality, the optimization of life histories can lead to increases in reproductive effort and associated increases in intrinsic mortality rates with age. When reproductive costs accumulate selection favours organisms that divert more of their resources to reproduction and less to maintenance as they grow older. Thus the physiological state of the organisms can deteriorate for adaptive reasons, and without any necessary involvement of genetic effects such as antagonistic pleiotropy or mutation accumulation. A tradeoff between reproduction and mortality suffices to produce the pattern of mortality rates that increase with age and reproductive rates that decrease with age. Furthermore, given senescent tradeoff structures, in which reproductive tradeoffs and physiological constraints become more severe with age, the optimal life history may produce mortality and fecundity schedules from which senescence would not necessarily be inferred. Thus senescent genetic effects may produce patterns similar to those observed for optimal life histories with constant tradeoffs, and there is no simple correspondence between senescence and patterns of phenotypic variation: the same patterns can be produced by senescent as well as by non-senescent organisms. This analysis suggests that the following is a key question: How and why do tradeoff structures change as organisms age?

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Energetic metabolism and habitat competition in *Nereis virens*.

The objective of this study was to examine the relationship between an individual's metabolic potential and its ability to gain possession of a habitat under a competition situation. We initiated twenty confrontations between two individuals of similar weight and size and identified a winner (the individual which occupied the burrow) and a loser for each encounter. We then measured enzyme activity (cytochrome c oxidase, lactate dehydrogenase, and pyruvate kinase), as well as, protein content, lipid content, and dry weight for each individual. There was no significant difference in enzyme activity between winners and losers but the duration of the competitive encounter was highly correlated with the energetic metabolism of the winners.

THE ALLOCATION OF RESOURCES TO REPRODUCTION IN *DAPHNIA*

34a.

T11

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One of the central themes of research in ecology in the past decades has been the variation in offspring size and number. According to the classic paper of Smith & Fretwell (1974), maximizing parental fitness will lead to a single optimal investment per offspring for any given environment. As the total effort per breeding attempt does not influence the parental fitness-function, changes in the total resource acquisition or in the proportion of the resources which is allocated to reproduction, are not expected to change this optimal investment per offspring. Organisms, living in changing environments with respect to food conditions, may, however, use their resource acquisition as an estimate of the environmental circumstances which their offspring will encounter after birth. Hence, planktonic cladocerans like *Daphnia*, mothers may assess the conditions their offspring will encounter, and adjust the offspring size according to the parent's resource availability.

In contrast to the predictions of the Smith & Fretwell model, I observed that large mothers produce larger offspring, and hence at a given food level juvenile size is dependent on maternal size. Several mechanisms have been proposed to explain this phenomenon. One explanation is that small juveniles are produced by small mothers to be able to avoid the effect of positively size-selective fish predation. Another explanation given in the literature is that larger animals produce larger juveniles as a result of the higher likelihood of intraspecific competition, and of predation by negatively size-selective invertebrate predators when large (=old) females are present. Both factors would result in higher mortality risks for smaller offspring.

The explanations given above, however, are hampered by the fact that it is thus far unknown which age of the mother the optimal offspring size is produced in a certain environment. Therefore, an experiment was carried out which investigated the relationship between maternal age and the fitness of respective broods produced by these animals. The intrinsic rate of population increase, r , was chosen as a measurement of fitness. Although the fitness of successive broods increased, the size of the juveniles increased more, and hence the fitness per unit effort decreased with increasing age of the females. Hence, optimal offspring sizes were found for offspring produced by the first adult instars of *Daphnia*. This implies that no further explanation has to be found as to why juveniles produced by young mothers are so small, but rather more effort has to be put in explaining super-optimal sizes of juveniles produced by older individuals.

GENETIC MARKERS AND QUANTITATIVE GENETIC VARIATION IN A SELFING
PLANT SPECIES, *MEDICAGO TRUNCATULA* (LEGUMINOSAE): A COMPARATIVE
ANALYSIS OF POPULATION STRUCTURE.

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T16

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Using RAPD markers and one morphological marker, we studied the among and within population structure in a selfing annual plant species, *Medicago truncatula* GAERTN. About 200 individuals, sampled from four populations subdivided into three subpopulations each, were scored for 22 markers. Unexpectedly, it was found that within population variance component accounted for 55% of the total variance, while among populations variance component accounted for only 45%. Eighteen percent of the total variance was due to within population structure. Thus, 37% of the total variance was within subpopulation. This large within subpopulation variance could be explained by either small neighborhood sizes within subpopulations, or by outcrossing following migration events, or both. Using a multilocus approach, it was found that no multilocus genotype was common to two populations. Two of the four studied populations were composed of a few lines (*i. e.* multilocus genotypes), whereas the other two had more multilocus genotypes than one might expect in a selfing species. In the most polymorphic population, only one genotype was found common to two subpopulations. By drawing a minimum spanning network of these multilocus genotypes, we could suggest migration events among these subpopulations. Resampling experiments show that, depending on the population, 3 to 16 polymorphic loci were necessary and sufficient to score all multilocus lines of the population. When these data are compared to published results, it appears that in some occasions, the number of genotypes per population of selfing species might be larger than would be expected from the sole consideration of population effective size. On the basis of these results, we chose the two most polymorphic populations to compare, at a fine spatial scale, the between and within population structure for quantitative and neutral characters. It was found that populations are more differentiated for metrics traits than for markers, and that the within population variability of these characters is reduced as compared to markers. These results suggest that: 1- between population, a stronger heterogeneous selection is acting on life-history traits than on markers, 2- within population, a homogenizing selection is acting on life-history traits, thereby reducing within population variability, as compared to markers.

16 **Queen-male conflict over mating in eusocial Hymenoptera: eager females and reluctant males?** T8

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Recent empirical evidence has shown that workers of ants, bees, and wasps can capitalise on relative colony-level differences in relatedness asymmetry by producing split sex ratios of remarkable accuracy. When such population wide variation in relatedness asymmetry is due to single colony-queens mating with either one or two males, this may lead to an evolutionary conflicts between gynes (prosepective queens) and males over the preferred number of matings. When later offspring-workers assess the proportion off full-sibs and half-sibs in their own colony and predictably produce mostly or only males in the more genetically diverse colonies dominated by half-sib relatednesses, gynes are under selection to go for one extra mating, because a male biased offspring sex ratio gives them a much higher fitness when the population sex ratio as a whole is still female biased. This fitness gain is frequency dependent, but can compensate for considerable costs of an additional mating as long as double mating is rare. Males, however, may find themselves in an opposite situation. Due to haplodiploidy, they have zero fitness when their worker offspring will later produce only new sterile workers and male sexuals. Under some scenarios, this should make males critical as to whether they should mate with an already inseminated gyne, and if they do so, as to how much sperm they should transfer. Optimal male strategies can then be predicted to depend on their chance to find alternative virgin mates in the same mating swarm, on the relatedness assessment accuracy of workers as a function of the relative sperm contributions of two males mating with the same queen, and on the frequency of double mating in the population as a whole.

Social insect mating strategies as we can observe them in the field may represent cumulative and frequency dependent equilibrium compromises between the contrasting interests of the sexes. However, the direction of sexual selection driving these dynamic equilibria is quite peculiar, as the conflict over mating implies that females should rather uncritically accept extra matings, whereas males should be critically trying to avoid wasting sperm on non-virgin females, whose offspring will destroy their fitness. Thus, workers winning the worker-queen conflict over the sex ratio from their mother-queens may have created a new evolutionary conflict over mating where prosepective mother-queens can reduce or eliminate the worker-queen conflict over the sex ratio by mating one more time, at the detriment of the fitness interests of their mates.

Molecular diversity of *Wolbachia*, endosymbionts of Crustaceans

303/37
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IT 14

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Wolbachia are strictly endocellular, vertically transmitted bacteria associated with insects and crustaceans. They are responsible for feminization, cytoplasmic incompatibility or parthenogenesis in their hosts, which enable them to increase their transmission in the host populations. By using PCR diagnostic primers we have found *Wolbachia* in 17 isopods : *Wolbachia* is widespread in Oniscidea occurring in all families and is also present in Asellota and Flabellifera. The taxonomic status of these microorganisms has been defined by sequencing parts of their 16S rDNA. *Wolbachia* are all closely related and form a monophyletic group which belong to the α -subdivision of purple bacteria. The most closely related genera are also endocytobiotic bacteria such as *Rickettsia*, *Ehrlichia* or *Anaplasma*. The bacteria from Oniscidea hosts show a very low divergence whereas bacteria from Asellota and Flabellifera are more close to the *Wolbachia* responsible for parthenogenesis in insects. The lack of concordance between bacterial and host phylogenies indicates that the crustacean-infecting *Wolbachia* have undergone horizontal transfer amongst arthropod lineages.

Other results including success of cross-infections with *Wolbachia* strains are consistent with the view that horizontal transfer has been predominant in the modern distribution of *Wolbachia*. These results show that horizontal interspecific transfers can contribute significantly to the wide distribution of *Wolbachia* within terrestrial isopods.

B chromosomes: a classic case of selfish genetic elements?

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B chromosomes were the first case of selfish genetic elements to be described some fifty years ago. In many species, B chromosomes are good candidates for selfish elements as they can accumulate during mitotic and meiotic nuclear divisions, thereby exhibiting 'drive'. Surprisingly, however, in view of the widely held belief that B chromosomes are universally selfish, it is now clear that B chromosomes in a significant number of species do not show drive, and in these cases their maintenance must depend on an enhanced fitness of their hosts.

This is the situation in *Allium schoenoprasum* at the River Wye, Powys, Wales, where B chromosomes occur in 65% of plants yet lack an effective drive mechanism. Their tendency to decline in frequency during transmission is counterbalanced by a selective advantage that they give their hosts in terms of early germination and a greater ability to germinate and survive under drought conditions. Clearly B chromosomes in *A. schoenoprasum* at the River Wye cannot be classed as selfish genetic elements.

B chromosomes also occur at an exceptionally high frequency (87%) in a neighbouring population of *A. schoenoprasum* on the River Irton, a tributary of the River Wye. Cytological evidence suggests that the Bs from the two populations have a common origin, yet the Bs at the River Irton, in contrast to those at the River Wye, behave as selfish genetic elements and show drive. This suggests that B transmission may be influenced by modifier genes on the A chromosomes, and highlights the possibility of a 'coevolutionary race' between the A and B chromosomes. The presence of contrasting B chromosomes in *A. schoenoprasum* provides an opportunity to investigate, within a single species, the evolutionary dynamics of both selfish and unselfish genetic elements.

Ectoparasitism as a factor of habitat selection in a colonial bird.

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Parasitism has largely been studied in the context of sexual selection, but its importance as a potential factor of habitat selection has little been considered. We presents the results of a long-term study on the population dynamic consequences of ectoparasitism by the tick *Ixodes uriae* on its host, the Kittiwake *Rissa tridactyla*. *Ixodes uriae* is an haematophagous ectoparasite which spends almost all its life in the cliff substrate, and feed on its seabird hosts when they come to land for breeding. The Kittiwake is a long-lived seabird which breeds in colonies situated on vertical seacliffs. A systematic monitoring of the host demography and behaviour, and of the parasite population dynamics was carried out over a period of 12 years. Each year, ticks were counted on the chicks at ringing. This allowed us to investigate the correlations between level of tick infestation and Kittiwake local demography and behaviour, but also the spatio-temporal dynamics of the ticks. Moreover, a parasite removal experiment was carried out in 1993 in order to investigate the causal nature of the relationships.

At the individual level, a lower probability of reproductive success was found associated with higher parasite load after correcting for the age of the chicks. Following the tick removal experiment, a higher index of reproductive success was found for nests of the sprayed areas compared to the control areas. At the cliff level, the density and prevalence of infestation of the cliffs were found negatively correlated with their reproductive success, taking into account the year, the local predator pressure and the cliff. Nests highly parasitized a given year were less likely to be re-occupied the following year, which can be explained by a lower probability of nest re-occupation following breeding failure. Higher host increasing rates were found associated with lower parasite levels of infestation. This can be explained by a higher recruitment of breeders on previous year successfull places. Finally, ticks were found heterogeneously distributed in space and there was a year to year temporal autocorrelation of cliff tick infestation.

Ectoparasitism by ticks appears to be a predictable factor of environment quality that not only affects the local reproductive success of its host, but also host dispersal and recruitment, and thus host metapopulation functioning. Together with predation, ectoparasitism is likely to be an important factor of habitat selection in group living species.

Dominance level influenced by environmental conditions

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Dominance level of an insecticide resistance gene (an insensitive acetylcholinesterase) in the mosquito *Culex pipiens* was found very different in two environments, varying from near dominance to near recessivity. To better understand this plastic response, various environmental parameters were manipulated and their interactions studied. Causal relationships were also explored. Results are discussed in the context of the various theories of the evolution of dominance.

SELECTIVE SWEEP OF Y CHROMOSOME AND GENETIC INCOMPATIBILITIES IN THE HOUSE MOUSE: SELFISH GENES IN ACTION?

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There is substantial genetic evidence that the three parapatric subspecies of house mouse (*Mus musculus*) found and characterised at the periphery of Eurasia are the result of a geographic radiation from a Northern Indian cradle several hundred thousand years ago. Each subspecies is characterised by one of the three mtDNA lineages, but possesses one of only two Y chromosome lineages (or types) existing in the whole species. *M. m. domesticus* and *M. m. musculus* have different Y types. The narrowness of the Y chromosome cline in their hybrid zone indicates a strong involvement of this chromosome in genetic incompatibilities between these taxa. We provide evidence from Y chromosome intron sequences that the divergence of these two Y lineages is much more recent than the radiation of the subspecies, and that the present subspecies distribution of Y types results from a recent sweep of one of them across subspecies. Furthermore the sex determination locus (*sry*) appears to show an exceptionally high non-synonymous substitution rate, particularly in one lineage. This is strong evidence that the evolution of the Y chromosome in this species has been driven by positive Darwinian selection that has caused the rapid spread of new haplotypes. We will review the evidence that the present distribution of Y types in *M. musculus* might result from the accumulation selfish genes on the Y and that this has contributed to the development of genetic incompatibilities between subspecies.

Fluctuating asymmetry (FA), the non-directional deviation from bilateral symmetry, is increasingly used as a measure of developmental stability and there is a strong trend towards using such measures as a 'general health certificate' of individuals or populations. However, the genetical and developmental basis of FA remains unclear. This paper will report on preliminary studies designed to address these issues for the pattern of eyespots on the left and right wings of the butterfly Bicyclus anynana. We have a good understanding of the developmental mechanisms underlying variation in the size and pattern of an individual eyespot. Each one has concentric rings of scale cells with different colour pigments which are synthesised in late pupae; determination of cell fate occurs in early pupae and involves establishment of an information gradient from a central 'focus' followed by an interpretation of the gradient by the surrounding cells. This paper will report on: 1) measurements of FA for eyespot size in inbred bottlenecked-lines and outbred control-lines; 2) a selection experiment on FA and 3) a comparative analysis of FA for eyespots which express either high or low phenotypic plasticity or for which visual selection from predators is known to be strong or weak.

Developmental stability, genetics and eyespot formation on *Bicyclus* wings

Brakefield P, Breuker C, Kesbeke F & Saccheri I

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Bicyclus anynana exhibits strong phenotypic plasticity in the form of seasonal polyphenism. Butterflies of the wet season form have marginal eyespots and a transverse band which are more or less absent in the dry season form. Short or long larval development times (e.g. at high or low temperatures) yield, respectively, these adult phenotypes. A similar phenotypic correlation is also observed for quantitative variation in phenotype within a cohort reared at a particular temperature. Selected lines have been established which produce either one form or the other (but not both) across all rearing temperatures. Experiments in which morphological eyespot traits or pre-adult development time of the butterflies are subjected to truncation selection consistently produce correlated responses in both sets of traits; larger eyespots and rapid development or the reverse. Evidence will be presented that this is due to a common mediation of the traits involving ecdysteroid hormones. It is argued that the form of the covariances is deeply imbedded in the phylogeny of the species-group and is utilized in an evolutionary sense when there is a fit between this form and the functional requirements of the environment. This will be discussed in the context of constraints.

Interactions between morphological and life history traits and the evolution of plasticity in tropical butterflies

Brakefield P, Kesbeke F & Koch PB

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Evidence for Genetic Hitchhiking at the *erect wing* Locus of *Drosophila melanogaster*. J.M. Braverman, C.H. Langley, and M. Aguadé. Universitat de Barcelona, Spain, and the University of California at Davis, U.S.A.

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An extremely low level of naturally occurring DNA sequence variation was observed in a survey of the *erect wing* locus of *Drosophila melanogaster*. This locus is located distal to *yellow* at the tip of the X chromosome, where the rate of crossing over per physical distance is severely restricted. Thus *erect wing* is an ideal place to test the hitchhiking model's two major predictions: a reduction in variation and an excess of rare polymorphic sites than expected under neutrality. The efficient single-stranded conformational polymorphism (SSCP) and stratified sequencing methods were used. The following results are based on the one kilobase surveyed to date. No variation was detected in samples from California, North Carolina, and Europe ($n = 50$ each), and the Zimbabwe population ($n = 50$) had only five polymorphic nucleotide sites ($\hat{\theta} = 0.001$, $\hat{\pi} = 0.0002$) and three insertion/deletion polymorphisms. Statistical evidence is presented that this reduction continues the trend of decreasing levels of variation along the tip of the *Drosophila* X toward the telomere. A skew in the frequency spectrum toward an excess of rare segregating sites at *erect wing* is supported by several statistics including Tajima's D ($D = -1.91$). In contrast to all loci previously surveyed from Zimbabwe, and departing from certain results for other loci located at the tip of the X, *erect wing* meets the two major predictions of the hitchhiking model. This data is used to estimate the parameters of a coalescent-based simulation of hitchhiking, and different versions of this model are compared to infer the relative locations of selected sites and *erect wing*, i.e., meiotic drive at the telomere or selected substitutions falling at random distances on either side of the *erect wing* locus.

Chromosomal clines in the Danish hybrid zone between European house mice

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The existence of 3 pairs of Robertsonian (Rb) translocations in *Mus musculus domesticus* mice from the hybrid zone in Denmark has allowed to analyze the interaction of these rearrangements with a chromosomally conservative genome, *M. m. musculus*. The cytogenetic analysis confirmed the non-introgression of the Rb fusions into the *musculus* genome. The geographic distribution of these Rb fusions follows three staggered chromosomal clines which increase in steepness the closer they are to the center of the hybrid zone as defined by allozymes. Analysis of alternate hypotheses suggests that chromosomal differentiation of the Danish *domesticus* occurred after contact was established with *musculus*. The staggering of the clines would reflect the order of arrival of the Rb fusions into the hybrid zone. Several models involving selection and diffusion processes are discussed to account for the difference in width between clines. A selective model with increasing levels of counterselection due to interaction with a progressively enriched *musculus* genome provides the best fit for the observed pattern. Counterselection of Rb fusions with little effect on the recombination of linked allozyme markers supports the view that only the centromeric segments of the Rb fusions are incompatible with the *musculus* genome.

To determine if limitation in centromere flow applied to non-Rb chromosomes as well, the distribution of silver-stained NORs (nucleolus organizing regions) was analyzed through the hybrid zone. Results indicated a clinal variation in the activity of a centromeric NOR present on chromosome 11 (NOR11) of *musculus* (maximum frequency: 80%) and absent in *domesticus*. The non-detection of NOR11 activity in *domesticus* mice was confirmed to be due to the absence of ribosomal genes on this chromosome, both by silver-staining of laboratory F1 hybrids (no dominance) and by *in situ* hybridization. The abrupt transition in frequency from 75% to 0% of this marker occurred over less than 3km and coincided with the center of one of the Rb clines. These results suggest that introgression of the centromeric region of the non-Rb chromosome 11 of *musculus* is also restricted. However, analysis of additional centromeric markers are needed to extend the hypothesis of centromere incompatibilities to the whole chromosomal complements of the two subspecies.

A Sequential-Arrivals Model of Territory Acquisition

authors: M.Broom, C.Cannings, and G.T.Vickers

It is not uncommon among birds for large numbers to nest close together. For example there may be thousands of kittiwakes nesting on a sea-cliff. At the beginning of a nesting season, birds (or more properly breeding pairs) have to establish themselves on a nest site. These sites will not all have the same value (as measured by the expected number of offspring) because of access by predators, the degree of shelter, inherent suitability etc. This paper describes a model of such a situation.

Birds arrive sequentially at a breeding area. The birds must decide whether to occupy a free site or contest for an already occupied one. In the latter case the odds favour the occupier, the loser incurs a cost and must go to a vacant site. It is of interest to find the optimal strategy for such a population. For any parameter values there is a threshold phenomenon: early arrivals occupy vacant sites, late arrivals fight. This result is intuitively reasonable, but the sequence of sites chosen is fairly complex. A recursive method for specifying the solution is given together with various examples.

It seems unreasonable that such complicated strategies could evolve. Various simpler classes of strategy have been considered. In particular we describe a case where an unreasonable looking strategy cannot be invaded directly, and the presence of a catalyst strategy is required to displace it.

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Methods for estimating the frequency of sex (ξ) in diploid organisms are based on the principle that sex restores Hardy-Weinberg equilibrium. This is clearly not applicable to haploid organisms. We have devised a method of estimating ξ of sex in haploids, based on gametic disequilibrium (D) being reduced by sex; in a single, completely sexual generation, D between unlinked genes is halved.

In the diploid case, the equations for estimating ξ are generally straightforward. Moreover, different, unlinked genes can be treated as replicate observations, so that a confidence interval for ξ can be found. In the haploid case, the equations which describe the transition of genotype frequencies through a sexual cycle are much more complicated, because of interactions between genes in a multi-locus model. Estimating all the parameters of the model - ξ and the set of genotype frequencies, $\{p\}$ - is difficult for two genes and impossible for three or more. Further, different genes clearly cannot be treated as replicates of one another in a multi-locus model, which precludes their use in finding confidence limits for ξ .

We estimate ξ using profile likelihood, a method which finds the maximum likelihood estimate of ξ while treating $\{p\}$, which need not be estimated, as nuisance parameters. Profile likelihood is based on standard likelihood theory, but is computer-intensive because ξ must be estimated for a large number of values of $\{p\}$. It is also possible to estimate additional parameters, such as a selection coefficient or a frequency of migration, at the same time as estimating ξ . Additional information can be obtained if the sexes of the individuals in the sample can be determined. The sample sizes needed for meaningful estimates of ξ will be discussed.

Profile likelihood may well have other, useful applications in population genetics, by allowing estimates of parameters of multi-locus and other complicated models.

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Several theoretical models involving matching host resistance genes and parasite virulence genes have been studied, by Leonard, Jayakar, Clarke, Barrett and others. In a wide range of models, gene frequencies evolve towards a form of stable limit cycle. Starting from low frequencies of both genes, (a) the frequency of a resistance gene rises because it the host with protection against most of the parasite population; (b) the matching virulence gene is selected because it allows the parasite to overcome the resistance; (c) the resistance gene confers reduced fitness if it is not effective against the parasite population, so its frequency falls; (d) the frequency of the virulence gene falls, due to adverse selection, since it is now not required for infection of the host.

There are numerous, well-studied examples of matching resistance and virulence genes, following Flor's "gene-for-gene" relationship, in plant diseases. There is also a considerable body of data on the frequencies of these genes in agriculture, notably in the rust and powdery mildew diseases of cereals. In some cases, the paradigm of a stable limit cycle has occurred. However, the mechanisms underlying the cyclical dynamics are not necessarily the same as those proposed by the theoreticians. Firstly, we must consider the selection of crop varieties by plant breeders, agronomists, seed merchants and farmers. Secondly, the question of selection against unnecessary resistance or virulence is controversial, because there is no evidence for it as a general phenomenon (although particular cases are known). Thirdly, linkage between genes and the existence (or not) of sex affects the dynamics.

Examples of cyclical and non-cyclical dynamics will be presented, illustrated by the powdery mildew disease of barley. These examples will be discussed in relation to genetic and cultural factors which cause evolution of crops and their diseases, and theoretical models which show how the persistence of polymorphisms in host and pathogen populations is affected by such factors as the frequency of sex and linkage between genes.

It is important to realise that plant breeders select varieties for many characters, including resistance to several diseases. The effort which a breeder puts into selecting for resistance to a particular disease depends on his or her perception of the importance of that disease. Coevolution of disease resistances and breeders' ratings of the importance of diseases leads to another kind of cyclical evolution.

MOLECULAR PHYLOGENY OF THE FAMILY APHIDIDAE BASED ON
DIFFERENT SUBUNITS OF THE F-ATPase COMPLEX

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Endosymbiosis is a key process in the evolution and speciation of aphids. As a consequence of this process at least three different genomes coexist in the same individual, i.e. nuclear, mitochondrial and the aphid endosymbiont (*Buchnera aphidicola*) genome. In the present work we analyse genes corresponding to the F-ATPase complex from the three genomes belonging to different species of the family Aphididae: the nuclear beta subunit, the endosymbiont *atpD* gene and the mitochondrial ATPase 6.

Molecular phylogenies based on different procedures, mostly character- and distance-based methods, are obtained and compared to determine possible cospeciation and/or coevolutionary events. Our results will also be discussed with those obtained by Moran et al. (1993, Proc. R. Soc. London B, 253:167-171)), who compared the phylogeny based on 16S ribosomal RNA genes from bacterial endosymbionts with the evolution of aphids based on morphological traits.

**Analysis of the terrestrial habitat component in a *Bombina*
hybrid zone using remote sensing**

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The hybrid zone between *Bombina bombina* and *Bombina variegata* in the Pescenica area, Croatia, differs in some respect from its counterpart in Poland. It is generally wider than the Polish one and is not strictly located at the transition from hills to plain, but bulges out into a lowland forest area. A possible cause for this difference lies in the continuation of habitat preferred by *B. variegata* into the plain (MacCallum, PhD thesis). By analysing environmental data taken from a Spot satellite image and topographical maps we intend to show the effect of habitat preference on the shape and position of the hybrid zone.

METAPOPULATIONS: AN APPROPRIATE FRAMEWORK FOR STUDYING THE DYNAMICS OF SPATIALLY DISPERSED HOST-PATHOGEN INTERACTIONS

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The interactions that occur between plants and their pathogens typically show considerable temporal and spatial variability. Much of this variability is generated by an underlying patchiness in the distribution of host demes and hence, inevitably, in those of their pathogens. This patchiness provides the ecological setting in which host-pathogen associations occur and has profound consequences for the long-term dynamics of co-evolved host-pathogen interactions.

Studies of interactions at the level of individual demes provide a picture of the immediate selective pressures that pathogen and host populations may exert on each other. However, for very many associations, such individual population interactions are inherently unstable with pathogen and, to a lesser extent, host populations undergoing periodic extinction. Within a population the chance of pathogen extinction is a function of the severity of the population crash, the size of the host population and the ability of the pathogen to survive unfavourable periods.

The extinction of individual demes highlights the importance of migration events in the re-establishment of interactions between hosts and pathogens and in providing a source of new variation in existing ones. The probability of migration events is clearly influenced by the size and proximity of neighbouring demes. Even when population crashes are not accompanied by extinction, genetic changes may occur in either host or pathogen population as a result of random genetic drift. In turn these changes may also alter the direction and intensity of selection. Depending on the frequency of migration, the numerical and genetical dynamics of individual populations are more or less independent of one another.

The consequences of this interplay of demographic and genetic forces is a model of evolution in a variable environment. Here coevolution is seen as a regional or metapopulation based process governed by a combination of drift, gene flow, and various forms of selection.

Two host-pathogen systems (*Filipendula ulmaria* as host to *Triphragmium ulmariae*, and *Linum marginale* as host to *Melampsora lini*) provide empirical evidence of the appropriateness of this model for addressing the evolutionary dynamics of natural host-pathogen systems.

Geographic variation of *Drosophila melanogaster* populations from the former USSR for enzyme loci and quantitative traits

Variation in eight enzyme loci (*Acph*, *Adh*, *Est-6*, *Est-C*, α -*Gpdh*, NADPH-dependent *dh*, *6-Pgd*, and *Pgm*) and four quantitative traits (wing size, wing shape, developmental rate, and productivity) was assessed in natural populations of *Drosophila melanogaster* from the territory of the former USSR (European region, the Caucasus, and Central Asia) that was previously poorly investigated with regard to *Drosophila* variation. The *Adh-F* allele frequency and wing size were shown to decrease in clinal fashion from northwest to southeast and were negatively correlated with temperature of the hottest calendar month. Productivity was higher in populations of Europe as compared to those of Central Asia; wing shape also was different between these regions. The existence of such differentiation in the territory where migration must be substantial suggests some selection pressure acting in natural populations of *D. melanogaster* in the northern part of the species range.

Geographic variation of *Drosophila melanogaster* populations from the former USSR for enzyme loci and quantitative traits

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Sex-Chromosome Polymorphism and Cytogenetics of Interpopulation Hybrids
in the Grasshopper *Podisma sapporensis* Shir.

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A comparative karyotype analysis of two populations of *Podisma sapporensis* has shown: $2n=22+XO$ and $2n=22+XX$, the X-chromosome is subacrocentric as result of the inversion within a population deviated from Sakhalin; $2n=20+neo-X+neo-Y$ and $2n=20+neo-XX$, as result X-autosome translocation in a population from Kurile (Kunashir island). The revealed karyomorphs of Sakhalin and Kunashir sex-chromosome races of *Podisma sapporensis* differ in structural rearrangements of the sex chromosomes in homozygous state. Simultaneously each of them differs discretely from the population of *Podisma sapporensis* of Hokkaido (Inoue 1985), the members of which have a standart acridid karyotype consisting of 23 acrocentric chromosomes in male, and 24 in female with sex determination XO/XX . The homozygous state of the revealed rearrangements in grasshoppers the group notable for conservatism of structural evolution of chromosomes allows to consider that the substantial role is played by isolation mechanism.

A field experiment in crossing between members of these populations showed the absence of precopulation isolation mechanisms, the embryos of the hybrid generation, however having been noticed to have mono- and trisomia by autosome, involved in the translocation. It caused permit to expect the disturbance in meiosis which would result in the formation of disbalance gametes and, therefore, sterility of hybrids.

This work was supported by a grant from Russian Fund of Basic Investigation (N 9-04-11606-a).

Molecular markers reveal cryptic sex in the human pathogen Coccidioides immitis

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Coccidioides immitis, cause of a recent epidemic of "Valley fever" in California, is typical of many eukaryotic microbes in that mating and meiosis have yet to be reported, but it is not clear if sex is truly absent or just cryptic. To find out, we have undertaken a population genetic study, using PCR amplification, screening for single strand conformation polymorphisms (SSCPs), and direct DNA sequencing, to find molecular markers with nucleotide-level resolution. Both population genetic and phylogenetic analyses indicate that C. immitis is almost completely recombining. These results motivate a directed search for mating and meiosis and illustrate the utility of SSCP and sequencing with arbitrary primer pairs (SWAPP) in molecular population genetics.

The origin and maintenance of London Underground (metro)
mosquitoes

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Subterranean and above-ground *Culex* have been given different species designations: *molestus* and *pipiens*. In Southern Europe the genetic evidence does not indicate the existence of two disjoint groups. Why have entomologists from Northern Europe distinguished the two groups? It may be that, in northern regions, the loss of diapause which occurs underground prevents establishment of above-ground satellites and hence acts to reduce gene flow in those regions with more severe climates.

Long-standing subterranean populations are therefore of particular interest. The London Underground (metro) has a long history of subterranean *Culex* dating back at least as far as the 39-45 war. Populations from the London Underground were sampled along with above-ground populations which were collected as near as practicable to each metro site. A genetic analysis of the populations by CAGE revealed clear patterns of genetic differentiation which imply at least some degree of reproductive isolation. The discrepancy with Southern European results will be discussed.

THE INFLUENCE OF PARTIAL INBREEDING ON EFFECTIVE
POPULATION SIZE AND FIXATION RATE IT 16
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The effects of partial inbreeding on effective population size and rates of fixation of mutant genes are investigated in selected populations. Predictions of effective size under an infinitesimal model of gene effects and directional truncation selection are given for partial selfing and partial full-sib mating. The joint effect of selection and partial inbreeding causes a large reduction in the effective size relative to the case of random mating. This effect is especially remarkable for small amounts of selected genetic variation. For example, for initial heritability 0.1 and proportion selected 1/6, the ratio of effective size to population size is 0.10 in populations with about 90% selfing while it is 0.85 in random mating populations. An experimental check of this effect is presented using an artificially selected isogenic population of *Drosophila melanogaster* in which there is a small amount of genetic variation in the selected trait due to a short period of spontaneous mutation. A consequence of the reduction in effective size is a proportional reduction in the probability of fixation of favourable mutants and a reduction in their time to fixation. Some recent results relative to the change in gene frequency of favourable alleles in partially inbred populations are discussed.

The *Anopheles gambiae* complex: contrasting phylogenies from nuclear and mitochondrial DNA sequences in mosquitoes

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The six Afrotropical species of mosquitoes in the *Anopheles gambiae* complex include the most efficient vectors of malaria, *A. gambiae* and *A. arabiensis*. These two species occur in sub-Saharan Africa, where they may occur in sympatry with each other or with any of the other species: *A. merus* and *A. melas* (east and west coast of central Africa, respectively), *A. quadriannulatus* (Ethiopia and Zanzibar), *A. bwambae* (Uganda). It has been speculated that speciation in this complex may be extremely recent (within 10,000 years) and introgression may occur among several of the species. Thus, phylogeny reconstruction has been quite difficult. The phylogeny based on paracentric chromosome inversions places the two principle vectors of malaria, *A. gambiae* and *A. arabiensis*, on two different clades. On the other hand, DNA sequence data from nuclear ribosomal DNA, two mtDNA coding regions (ND4 and ND5) and an esterase gene for five of these species strongly support the sister taxa relationship of *A. gambiae* and *A. arabiensis* and the mtDNA data further indicate the occurrence of gene flow across the two species. To try to clarify the relationships among the species we (1) added the mitochondrial A+T-rich region (potentially its rapid rate of evolution could provide the data to resolve the relationships of such closely related species) and (2) sequenced a segment close to the breakpoint of inversion 3a on the chromosome, to understand if the inversion, which clusters *A. gambiae* with *A. merus* and not *A. arabiensis*, is indeed monophyletic. The A+T-rich data confirms that *A. gambiae* and *A. arabiensis* are sister taxa, as shown by the other mtDNA data. The phylogeny based on the nuclear gene within the inversion supports the chromosomal phylogeny, with *A. gambiae* and *A. merus* as sister taxa.

The conflicting DNA data sets have very strong phylogenetic signal, yet produce different conclusions. Such contrast may be explained by gene flow between *A. gambiae* and *A. arabiensis*. This results in introgression of mtDNA genes and nuclear DNA outside the inversions, while some form of selection could prevent introgression for the DNA within the inversions. Thus, the DNA within the inversion may reflect the "true" phylogeny of the group. This data set emphasized that in some cases it may not be appropriate to use a "total evidence" approach to reconstruct phylogenies. These results also highlight the importance of knowing the chromosomal location of genes used in phylogenetic analysis and whether they are associated with chromosomal rearrangements such as inversions.

EVOLUTIONARY CONFLICTS WITH MULTIPLE CONTESTANTS

Most evolutionary conflicts are modelled as pair-wise contests. Most conflicts in practice will involve many contestants, e.g. sperm-competition, nest-site acquisition. A number of different scenarios for multi-contestant conflicts have been considered

- (i) The multiplayer War of Attrition,
 - (ii) the acquisition of nests in a breeding area,
 - (iii) sperm-competition,
- and a variety of possible structures developed.

In moving from two to many players the complexity of the solutions, whether as ESS's or in terms of the dynamics increases substantially. Results will be presented which illustrate both the potential complexity and the existence of certain types of cycling, and catalysis.

Phylogenetic and population studies on Canarian darkling beetles of the genera *Pimelia* and *Hegeter* (Tenebrionidae, Coleoptera) using mitochondrial DNA sequences.

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The Canary archipelago forms a volcanic island chain into the Atlantic off the North West African coast. A range of organisms have colonised the archipelago radiating through the islands to produce a series of endemic species and subspecies. The genera *Pimelia* and *Hegeter* comprise flightless saprophagous beetles with 14 and 22 endemic taxa, many of them present in one island only. A portion of the mitochondrial Cytochrome Oxidase subunit I gene (COI) has been used as a marker. DNA sequences (200-450 bp) have been obtained by automatic sequencing of PCR products on all *Pimelia* Canarian species and 17 species of *Hegeter* plus several continental outgroups. These data sets were analysed phylogenetically by maximum parsimony and distance approaches and the resulting trees used to deduce sequential inter-island colonisations compatible with the geological dating of the islands.

We sampled populations from the *Pimelia* species-complex of Tenerife *P. radula*, *P. r. ascendens*, *P. r. granulata* and *P. canariensis*; three subspecies from the *P. laevigata* distributed in the western islands (Gomera, La Palma and El Hierro), which are of more recent formation; and *Hegeter politus* from the older western islands (Fuerteventura, Lanzarote and their islets). Altogether, these samples represent some 180 individuals from more than 25 populations in which mitochondrial DNA sequence data has been obtained. The data has been analysed by various methods and phylogeographies produced. Sequence divergences are in accordance of the geological age of the islands and allow one to deduce patterns of intraspecific colonisation. Interestingly, in Tenerife there are two diverged mitochondrial types not concordant with the morphological species, suggesting that the geological history of the island has influenced the present distribution of mitochondrial genotypes within the island.

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HABITAT CONDITIONS AS POTENTIAL FACTORS AFFECTING REPRODUCTIVE ISOLATION AMONG SYMPATRIC POPULATIONS OF ROTIFERS

In a previous study it was reported on the genetic structure of populations belonging to the species complex *Brachionus plicatilis* (Rotifera) in Torreblanca Marsh (Castellón, Spain). Three clonal groups, called SS, SM, and L, which differed both in their allozyme patterns and morphology, were found in an annual cycle survey of allozyme variation and population structure. These clonal groups were involved in a seasonal succession in one of the ponds studied, and temporal and spatial distribution suggest ecological specialization of the genotypes. Allozyme data provided no trace of gene flow among clonal groups, although SS and L clonal group, on one hand, and SM and L groups on the other, showed partial overlapping sexual periods. Experimental studies pointed out that behavioral reproductive isolation can account for the absence of interbreeding among these clonal groups. In contrast, SS and SM clonal groups showed lower levels of behavioral reproductive isolation. Spatial and temporal distribution, and sexual periods of these two clonal groups seems to be more segregated in the wild. Observations of natural populations also suggested that different clonal groups might induce bisexual reproductive periods at different population densities.

Our objective in this contribution is to study the ecological specialization of clonal groups to determine the role of ecological factors in the segregation of sexual periods among clonal groups and thus to evaluate the importance of habitat or seasonal isolation on the absence of interbreeding. We conducted this work studying differences in life history traits (i.e. population growth rates and induction of bisexual reproduction) among clonal groups growing in several conditions of salinity and temperature, the main environmental abiotic parameters that showing variation in the habitat where rotifers were isolated.

Results showed genetic variation in the population density threshold for bisexual reproduction induction, the differences among genotypes being modulated by salinity and temperature. These results are discussed focusing on the importance of seasonal or habitat reproductive isolation among clonal groups in Torreblanca Marsh.

Change in genetic architecture resulting from the evolution of insecticide resistance

Carriere Y & Roff DA

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Strong directional selection for insecticide resistance in agricultural systems favours an increase in frequency of resistance allele (s). A resistance allele, however, may have strong pleiotropic effects on life history characters. A model is developed showing that the spread of such an allele induces a change in the mean and in the additive genetic variance (heritability) of life history characters, and in the genetic covariance (correlation) between these characters. As resistance develops from an initial value of zero, the model predicts a positive relationship between the degree of resistance within the populations and, 1) the magnitude of the fitness costs, 2) the heritability of the life history traits, and 3) the absolute value of the genetic correlations between pairs of life history traits. The model was tested using a quantitative genetic study that compared, in a lepidopteran species, the genetic architecture of diapause propensity and larval weight within and among insecticide-free and insecticide-treated populations from the same geographic area. All the predictions of the model were confirmed, suggesting that the novel evolution of insecticide resistance results in major changes in the genetic architecture of fitness, which may limit to some extent the colonisation of insecticide-treated habitats.

A multi-technique approach to the study of genetic structure of Mediterranean populations of the sea bass *Dicentrarchus labrax*

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The European sea bass *Dicentrarchus labrax* is the object of extensive research in our laboratory aimed to elucidate the genetic structure of wild and cultivated populations, and to search for historical and dynamic causes of their genetic diversity. This poster compares the results of genetic analyses of reared samples before and after experimental acclimation to freshwater to a study of wild Mediterranean populations from both coastal lagoons and sea. Three different technical approaches (allozymes, RAPD markers and mtDNA length variation) were used to investigate the levels of genetic polymorphism and heterogeneity within and among populations.

Acclimation trials were repeated for two years (1989, 1990) starting from the same broodstock. Results from these experiments showed that survival to acclimation to freshwater was not random with respect to both allozyme genotype and RAPD markers. At least for allozymes these results strongly suggested the hypothesis that regimes associated with acclimation trials selected within an heterogeneous array of genotypes, probably reflecting the different geographic origin of broodstock (Allegrucci et al., 1994). As for RAPD markers, statistical chance of concordant change for few markers out of 126 was more difficult to dismiss (Allegrucci et al., 1995).

Results from these experiments led us to explore the pattern of geographic variation in a sample of wild Mediterranean populations and to assess whether ecological differences between marine and lagoon populations also reflect genetic heterogeneities at the same "selective" markers as in the acclimation experiments. Therefore the pattern of variation of each marker has been investigated in respect of both ecology and geography. Indeed, selective agents seem to play a role in determining different genotype arrangements in coastal lagoon and marine populations, as the results from certain allozyme loci and RAPD markers suggest. However, there is also a strong geographic component due to the remaining set of "neutral" loci including both allozymes and RAPD markers.

The third marker, mtDNA D-loop, also showed differential survival of mtDNA genotypes in acclimation experiments indicating that only a portion of the initial maternal lines were represented in the acclimated sample. A large array of genotypic diversity was revealed within all natural populations, being 46% of examined individuals heteroplasmic for up to four different D-loop size classes.

61a.

P8

Nutrition, age at reproduction and the cost of mating in female
Drosophila melanogaster.

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Multiple mating by females could have several evolutionary explanations. In *Drosophila melanogaster* females, remating is necessary to maintain maximum fertility, but females that have high remating rates have reduced lifetime reproductive success. The cost of mating is caused by the transfer of non-sperm components of male seminal fluid to females at mating, and may represent a side-effect of evolutionary conflict between males. Females would be expected to evolve mating rates determined by the need to maximise fertility and to reduce the cost of mating.

We manipulated female mating rates by altering food levels and access to males, in order to determine the conditions under which the cost of mating disappeared. Females on the three highest nutritional levels showed survival costs of mating; however, only females kept on the highest food level incurred significant reproductive costs. We also investigated the evolution of female remating rate in lines selected on age at reproduction. Females from lines selected for late-age reproduction had significantly longer lifespans and lower remating rates than females selected for early-age reproduction. Increased 'tolerance' to males in lines selected for late-age reproduction may therefore be achieved by the evolution of lower mating rates that minimise mating costs.

**CHROMOSOMAL VARIATION IN THE BLACKFLY
ONCHOCERCIASIS VECTOR *SIMULIUM GUIANENSE*
IN BRAZIL**

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Simulium guianense is the primary vector of *Onchocerca volvulus* in the highland Amazonian focus of human onchocerciasis in Brazil. While being a voracious biter of humans in the focus, there are populations elsewhere where the species is zoophilic. As with many other morphospecies of *Simulium*, this difference in biting behaviour may be indicative of the presence of a sibling species complex. We present the initial results of an on-going study investigating the larval polytene chromosome banding pattern variation of *S. guianense* in Brazil. These preliminary results from five populations reveal the existence of four cytotypes indicating the potential for differentiation. Sex chromosome evolution in simuliids is highly correlated with speciation so that no two species/cytotypes share the same differentiated chromosomes, and in some cases only vary in their sex chromosomes. We describe in detail the chromosomal differences found among the four cytotypes and consider sex chromosome evolution in this complex.

Genetical structure at spawning and non-spawning season in a fish hybrid zone.

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Barbus barbus and *Barbus meridionalis* form an hybrid zone in a river in the south of France. Previous studies have described classical allozymic clines along the hybrid zone (Berrebi *et al.*, 1993). Linkage disequilibrium analysis revealed an excess of parental genetic combinations (Crespin, 1992), suggesting this hybrid zone might be a tension zone (*i.e.* a hybrid zone that is maintained by a balance between migration of parental genotypes from the edges and counterselection of hybrids). Many clues suggest fitness reduction in hybrids, among which F1 male sterility, revealed by controled crosses (Philippart & Berrebi, 1990). Captures/Recaptures have been undertaken by one of us (LC) for the last two years (1993 to 1995) and indicate large scale migrations are almost certainly absent.

An alternative, although not exclusive, explanation for linkage disequilibrium is constituted by homogamy. In effect, behavioural and ecological preferences can make reproduction between different types unlikely. Also, counter selection of hybrids may have caused the evolution of prezygotic barriers thus generating homogamy.

An analysis using several microsatellite loci (mendelian hypervariable markers) was performed on individuals from the median part of the cline. Two levels of structuration were studied: The reproductive group (individuals were recaptured in different spawning grounds), and the station as a whole. In addition the reproductive and non-reproductive seasons are compared at the station level. Homogamy could be revealed by intra-reproductive group genetic homogeneity. Temporal comparisons could suggest the presence (or absence) of slight migration during the spawning season.

Contribution to the classification of 32 acacia species with reference to their genome size determined by flow cytometry

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Dryland acacia species are represented by several taxa including numerous sub-species and synonyms (Ross 1979, Brenan 1983). The aim of this study is to contribute to enlighten classification among taxa through cytogenetic observations.

Besides chromosome counting, that appears to be difficult on these species (Shukor *et al.* 1994), flow cytometry provides a rapid and accurate method to determine mean nuclear DNA content of every studied taxon. When comparing these, it is possible to show different ploidy levels. Moreover, it is possible to classify the taxa according to their genome size (Hamon *et al.* 1992, Martinez *et al.* 1994, Blondon *et al.* 1994).

We measured 51 populations of acacia representing 32 different taxa originating from 13 countries in the sub tropical area. Each population is represented by 3 individuals. We measured two replicates of 2500 nuclei for each individual. An internal standard is provided by a human plasmocyt cell line with 6.54 pg DNA in 2C nucleus (Shambrook 1989). This allows calculation of the genome size of each individual.

The data collected were subjected to one way analysis of variance and multiple range analysis. Results show that 53% among the studied taxa belongs to a homogenous group with 1.01 pg/2C DNA (0.87~1.13). This group includes species known as diploid $2N=2C=26$ (Ross 1979): *A. senegal*, *A. dudgeoni*, *A. mellifera*, *A. gourmaensis*, *Acacia albida*. We determined that *A. tortilis raddiana* from Tunisia and *A. nilotica tomentosa* also belong to this diploid group. This leads to split these two taxa into groups with different ploidy level.

A second group with 2.97 pg/2C DNA (1.76~2.24) brings together tetraploid species (Ross 1979): *A. tortilis* from India, *A. nilotica adansonii*. We determined that *A. borleae* and *A. luederitzii* also belong to this group.

The third group is intermediate between both former groups with 1.55 pg/2C DNA (1.40~1.69). We consider that it brings together triploid species such as *A. laeta* (Ross 1979), *A. farnesiana* and *A. tortilis spirocarpa* from Tanzania also belong to this group.

At last, some taxa still stay unaffected to a described group. *A. tortilis raddiana* from Senegal, known as 4N or 8N shows 2.30 pg/2C DNA. This is significantly more than DNA content in the tetraploid group but much less than an expected 4 pg/2C DNA for an octoploid species. Same occurs with *A. hebeclada* known to be octoploid but showing "only" 2.49 pg/2C DNA in our study. This observation that genome size doesn't strictly follows the ploidy level is in accordance to several authors (Furuta *et al.* 1988).

This analysis shows that a large variability of the genome size occurs not only among species but also between subspecies of acacia. The results are compared to previous studies on genetic diversity of acacia populations using isozymic markers (Chevallier *et al.* 1994, Cardoso 1995). They are discussed in relation to the evolution within the genus *Acacia*.

ASYMMETRICAL INTROGRESSION BETWEEN *PAPILIO MACHAON* AND ITS ENDEMIC
SARDINIAN-CORSICAN RELATIVE *PAPILIO HOSPITON* (LEPIDOPTERA, PAPILIONIDAE)

64

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T17

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Sardinia and Corsica are inhabited by the endemic *Papilio hospiton* and by its Palaeoarctic relative *P. machaon*. Nei's average genetic distance between the two species, when allopatric, is about 0.40, while being about 0.30 when sympatric populations are compared. This is owing to the presence in the gene pool from Sardinia and Corsica of alleles characteristic of *P. hospiton* at a number of loci, whereas the reverse, introgression of *P. machaon* alleles in *P. hospiton*, is rare and mainly limited to the *Pgm* locus. As previously shown by Clarke & Sheppard (1955) and Clarke & Larsen (1986), F_1 hybrids between *P. machaon* and *P. hospiton* are easily obtained in the laboratory, (mainly by hand pairing), but are generally sterile and their eventual offspring are poorly or no vital at all. In the field, natural hybrids between the two species have been found at low frequency (1-2% in sympatric areas). The present features of hybrids and their offspring makes the level of gene flow between *P. machaon* and *P. hospiton* very low, if even present. This contrasts with the high introgression detected in *P. machaon* in Sardinia and Corsica (about 80% of *P. machaon* individuals from these areas show at least one *P. hospiton* allele at at least one of the differentiated loci), observed also in areas of the two islands where *P. hospiton* has not been found. The most likely hypothesis for this massive introgression involves past hybridization phenomena between *P. machaon* and *P. hospiton*, possibly occurred when these two taxa, differentiated allopatrically, came into secondary contact without having evolved effective isolating barriers. Pre-mating barriers (ecological differences, and especially assortative mating) as well as post-mating ones (hybrid sterility and low or null vitality of their offspring) have apparently been perfected in sympatry, possibly reinforcement phenomena, owing to hybrid unfitness.

INTROGRESSIVE HYBRIDIZATION BETWEEN ENDOPARASITE ASCARID WORMS
PHOCASCARIS PHOCAE HØST, 1932 AND *P. CYSTOPHORAE* BERLAND, 1964
 (NEMATODA, ASCARIDOIDEA)

65

T17

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A peculiar hybrid zone was evidenced between the seal ascaridoid endoparasites *Phocascaris phocae* Høst and *P. cystophorae* Berland, both in North-East and North-West Atlantic, with different proportions of the two parental types (characterized by alternative alleles at the loci *Sod-1*, *Est-1*, and *Mpi*) and of recombinant genotypes, (including F₁ and F_n hybrids, backcrosses and introgressed individuals) in different seal hosts and locations. In the hooded seal *Cystophora cristata*, "pure" *P. cystophorae* are largely prevailing, followed by recombinants, while "pure" *P. phocae* are very rare; in the grey seal *Halichoerus grypus*, *P. cystophorae* still prevails, although with a higher proportion of recombinants and of "pure" *P. phocae*. In the harp seal *Pagophilus groenlandicus*, *P. phocae* prevails, at least in NE Atlantic, and recombinants are relatively abundant. Last, in the ringed seal *Phoca hispida*, recombinant genotypes largely prevail over both parental species, and their gene pool proves to be in Hardy-Weinberg equilibrium. The available data suggest that *P. phocae* and *P. cystophorae* started to diverge allopatrically about half a million years ago, as estimated from their genetic distance (Nei's $D=0.11$), adapting to and coevolving with different definitive hosts: the harp and the hooded seals, respectively. Secondary contacts between these two seals and their *Phocascaris* parasites in the last interglacial led to introgressive hybridization between *P. phocae* and *P. cystophorae*. Hybrids and recombinants were presumably selected against over parental species in the respective definitive hosts of the latter, while being favoured in a new host, the ringed seal. Evolution of assortative mating in *P. phocae* and *P. cystophorae* seemingly took place, as indicated by the very rare occurrence of F₁ hybrids. Two possible evolutionary outcomes can be hypothesized for this hybrid zone: (1) maintenance of a dynamic equilibrium between *P. phocae*, *P. cystophorae* and their recombinants, gene flow being counterbalanced by differential selective pressures; (2) completion of reproductive isolation between *P. phocae* and *P. cystophorae*, while hybrid populations may give origin to a stabilized recombinant species, adapted to the ringed seal.

REPRODUCTIVE ISOLATION AND PARAPATRIC HABITAT DISPLACEMENT BETWEEN THE
SIBLING SPECIES *HYDROMANTES AMBROSII* AND *H. STRINATII*

(AMPHIBIA, PLETHODONTIDAE)

66.

T7

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The European plethodontid salamanders *Hydromantes ambrosii*, from Tuscany, and *H. strinatii*, from Liguria and Southern France are two sibling species until recently considered as subspecies of *H. italicus*. Field and genetic studies carried out in these years have evidenced that the two salamanders have a parapatric distribution north of La Spezia. In such area, populations of the two species can be recognized by fixed allele differences at 9 over the 34 enzyme loci analyzed, with no evidence of hybrid, recombinant or introgressed individuals. In the parapatric zone, habitat displacement has been detected between the two salamander species: *H. ambrosii* occurs only where thermophilous vegetation is present (evergreen sclerophyll woodlands and mediterranean maquis), whereas *H. strinatii* can be found in cooler and moister areas with a mesophyllous-temperate vegetation (deciduous woodlands of *Castanea sativa*). When allopatric, both taxa inhabit mainly mesophyllous-temperate woodlands. This parapatric habitat subdivision could be a result of competition, *H. strinatii* confining *H. ambrosii* in a habitat not occupied by the latter when alone. Field studies have shown that both species share similar ecological requirements: e.g. humid and cool subterranean refuges during the hot season, and availability of small invertebrates as preys. A transplantation experiment, making the two species artificially sympatric in the field (a cave located in the zone of parapatry, originally occupied by *H. strinatii*), was carried out by replacing about 50% of *H. strinatii* individuals with *H. ambrosii* specimens from another parapatric site. After three years, the collected data show that: i) *H. ambrosii* is still present in the transplantation area; ii) the two species are reproductively isolated (newborns of both species, electrophoretically identified, have been recorded, but no hybrids); iii) *H. strinatii* occupies, during the summer, the central part of the cave and confines *H. ambrosii* both near the adit (where temperature and moisture are more variable) and in the deepest part of the cave (where invertebrate preys are scarce). These preliminary data support the hypothesis of a habitat subdivision due to competition for cover (moist and cool refuges) and/or food, as previously demonstrated for other plethodontid salamanders (Jager, 1970, 1971).

Title:

Population genetics of the Komodo dragon *Varanus komodoensis*

Authors and addresses:

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Abstract:

The Komodo dragon *Varanus komodoensis* is an endemic species of monitor lizard of four south eastern Indonesian islands in the Lesser Sunda region. Habitat exploitation by ever-growing human activity and the depletion of prey species represent real problems for the Komodo dragon in maintaining its original range and indeed surviving.

The main goal of this study is to assess the degree of genetic variability through DNA analysis to reconstruct evolutionary relationships of natural populations of *V. komodoensis*. The research will contribute substantially to a comprehensive and scientifically rigorous base of knowledge, with which to assist the management of the species both in the wild and in captive breeding programs.

It will also try to clarify the phylogenetic position of *V. komodoensis*, and to re-examine the taxonomic status of the genus *Varanus*.

Seventy-eight individuals were caught in four islands during a three months field-work, in order to collect either blood or tissue samples. Analysis of sequence variation among individuals of the control region of the mitochondrial DNA and allele frequency differences at *microsatellites* loci is being carried out. The latter are short tandem repeats of sequence units of nuclear DNA which are highly polymorphic due to variation in the number of repeats and are rapidly becoming the marker of choice in population genetics studies.

Sampling techniques and preliminary results are provided.

The sex peptide in *Drosophila* : Evolution at the molecular level.

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The *Acp70A* gene codes for a male accessory gland peptide that is transferred to the female during copulation. To evaluate the role of the forces shaping variation at the *Acp* region, we have compared DNA sequence polymorphism and divergence both in the *melanogaster* and *obscura* groups of *Drosophila*.

In contrast to *D.melanogaster* and *D.sechellia* where *Acp* is a single copy gene, all the analysed species of the *obscura* group (*D.subobscura*, *D.guanche*, *D.madeirensis* and *D.bifasciata*) have a duplication that includes the coding and 5' flanking regions of the gene. Expression studies in adults of *D.subobscura* indicate that both copies are active, and that like in *D.melanogaster* they are only expressed in males.

Comparison at the protein level shows that the C-terminal part of the active peptide is highly conserved and that the signal peptide has the same length in all the species although the sequence differs between groups.

HETEROCHRONY AND EVOLUTIONARY CHANGE IN UPPER CAMBRIAN
OLENID TRILOBITES.

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(Department of Geology and Geophysics, University of Edinburgh)

Black shales, slowly but continuously deposited in anoxic conditions over long time periods may yield abundant fossils, and such sequences may be eminently suitable for detailed studies of microevolution.

In the Upper Cambrian of Scandinavia, the Alum Shale succession, some 80m thick, and deposited over some 20 million years, contains abundant trilobites belonging to the single family Olenidae, often in an excellent state of preservation. These shales were deposited on a largely stagnant sea floor, and the trilobites seem to have been adapted to a low oxygen level.

The abundance of specimens, their fine preservation (especially in calcareous concretions within the shale sequence), the condensed sequence, the potential for band-by-band collecting, and the fact that usually only a single, widespread species is present at each level (thus clarifying ancestor-descendant relationships, all allow an excellent potential for evolutionary research. This was recognised over sixty years ago in the pioneer studies of Kaufmann. But in addition, since the olenids often occur at all growth stages, the ontogenies of successive genera can be elucidated and it is then possible to establish whether heterochrony has been a significant factor in evolutionary change.

We have elucidated the ontogenies of the earliest olenid genus *Olenus*, and the descendant genus *Parabolina*, based upon material in calcareous concretions from old quarries in southern Sweden. Many of the apparently 'new' characters that appear in *Parabolina* are present in juvenile stages of *Olenus*, and are pedomorphic in origin, some other features arise by peramorphosis. The unique morphology of *Parabolina* is thus derived by mosaic heterochrony from the ancestral state. Band-by-band collecting in the shales through part of the same sequences shows that many characters change gradually, in other words we have a temporal pedomorphocline.

Whereas heterochrony has long been known to play an important role in evolutionary change, in trilobites as much as other organisms, such data, extended to higher levels within the sequence, may reveal the relative roles of paedo- and peramorphosis in an evolving lineage.

The role of sexual reproduction in the spread of viruses through fungal populations.

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Viruses are excluded from the sexual spores of virus containing fungi. Consequently the frequency of a virus in a fungal population will be decreased by sexual reproduction. To maintain itself in a fungal population a virus must compensate for this. There are three possible strategies for the maintenance of a virus in a fungus:

- 1) Infection of asexual fungi. Many asexual *Aspergillus* and *Penicillium* species contain viruses but viruses have never been observed in their sexual relatives.
- 2) A virus can compensate for absence in sexual progeny by increasing the asexual reproduction of its fungal host. This is observed in plant pathogenic fungi. Viruses often cause hypovirulence (decreased pathogenicity) in plant pathogenic fungi. Consequently the plant host of the virus infected fungus lives longer so that the fungus has more time to reproduce asexually.
- 3) Viruses can spread horizontally through fungal populations by vegetative fusion. However the vegetative incompatibility mechanism operating in most fungi could be a barrier to horizontal transfer.

To investigate the maintenance of a virus in a sexual fungus a virus was transferred from the asexual *A.niger* to the sexual *A.nidulans*. Natural viruses have never been observed in isolates of *A.nidulans*. Experiments gave the following results:

- 1) The virus did not influence growth or spore production of the fungus.
- 2) The virus was present in asexual spores but not in sexual spores.
- 3) The virus could be vegetatively transferred between heterokaryon incompatible strains.

Our conclusion is that although the virus does not lower the fitness of the fungus and can spread vegetatively the absence of virus in sexual spores explains why viruses are not found in the *A.nidulans* population.

Male dimorphism, alternative mating strategies and virginity in fig wasps

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Fig wasps develop in the fruits of *Ficus* spp. and can be divided into pollinating and non-pollinating species. Each of the 700 *Ficus* spp. has only one pollinator species but may host as many as 30 non-pollinating species. Female wasps are always winged. All pollinator males are wingless but the males of any given non-pollinator species may be all wingless, all winged, or a mixture of the two types. Wingless males are specialised for mating with females inside the natal fig while winged males disperse from the natal fig and mate with females in the tree canopy or elsewhere.

Using data on approximately 100 fig wasp species from South Africa, Panama & Australia, we show that mean brood size (number of wasps developing per fig) is a very strong predictor of male morphology. Species with large broods have wingless males, those with small brood sizes have winged males, and those with intermediate brood sizes have dimorphic males. The data are consistent with Hamilton's hypothesis that selection on the proportion of winged males is determined largely by the proportion of females (hereafter termed virgins) that leave their natal fig unmated. The key consequence of small brood size is that it increases the likelihood of virginity, thus selecting for winged males.

Despite the relationship described above, mean virginity ranges from 0-40% in species with wingless males. In these species, brood size explains most of the variance in %virginity. While species with broods >20 (including nearly all pollinators) have effectively 0% virginity, those with brood sizes <20 may experience substantial virginity levels. The re-evolution of winged males in species with wingless males, low brood sizes & high virginity may be subject to phylogenetic constraints. Wingless males in the genus *Otitella* have evolved an alternative to wings - they leave the fig and signal to attract conspecific females.

EXTRAORDINARY KARYOTYPIC VARIATION IN *APIOMORPHA*:
IS CHROMOSOMAL EVOLUTION DRIVING SPECIATION?

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Lyn Cook

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Apiomorpha (Hemiptera: Coccoidea: Eriococcidae) is a genus of scale insect in which both males and females induce galls on *Eucalyptus*. The galls induced by females of *Apiomorpha* are generally species-specific and those of some species are amongst the largest and most spectacular of all insect-induced galls. There are currently 39 morphospecies of *Apiomorpha* described.

Coccoids possess holokinetic chromosomes but, contrary to the assumption that holokinetic chromosomes show a great propensity for fragmentation, most coccoid families and genera have retained conservative chromosome number ranges. *Apiomorpha*, however, has been found to exhibit chromosome numbers ranging from $2n = 4$ to $2n = 164$. This range exceeds that previously reported for the whole of the Hemiptera.

Variation in diploid chromosome number has been found within 16 of the 24 morphospecies of *Apiomorpha* for which more than one population has been examined. In only six of these morphospecies has concomitant variation in morphology been detected. The large range of chromosome numbers found within several other morphospecies suggests that several cryptic species may be present.

Apiomorpha provides an opportunity to study the role of chromosomal evolution in speciation processes. If it can be demonstrated that chromosomal differences became fixed prior to morphological or genic changes becoming fixed, then chromosome change may be implicated as playing a primary causative role in the speciation of the chromosomally divergent taxa.

Genetic Diversity in the Horse. (Equus caballus)

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Genetic variation was examined in 84 distinct populations of domestic horse breeds and 36 feral horse populations. Over 8,100 individuals were examined. Seven red blood cell alloantigen loci (blood group loci) and 10 biochemical loci were examined for each individual. All loci were known to be polymorphic in horses. The primary variables analyzed were observed and expected heterozygosity (H_o and H_e) and effective number of alleles (ENA). In general, genetic variability was greater within domestic breeds than in feral populations. In domestic breeds, genetic variation was not statistically associated with population size of the breed. For feral herds, H_o was not significantly influenced by population size but H_e and ENA showed a statistically significant, positive association with population size. For both domestic and feral populations, there was unexpectedly high H_o in very small populations ($N < 1000$ for domestic breeds and $N < 100$ for feral herds). In general, variation measures related to allelic diversity tended to be associated with population size while individual variation was not. In feral populations, estimated inbreeding level (Wright's F_{is}) was significantly and positively associated with population size. That is, higher inbreeding levels were observed in larger populations. Almost all the smallest populations had negative F_{is} values. Overall, recent population size is not a good predictor of genetic variability in horse populations.

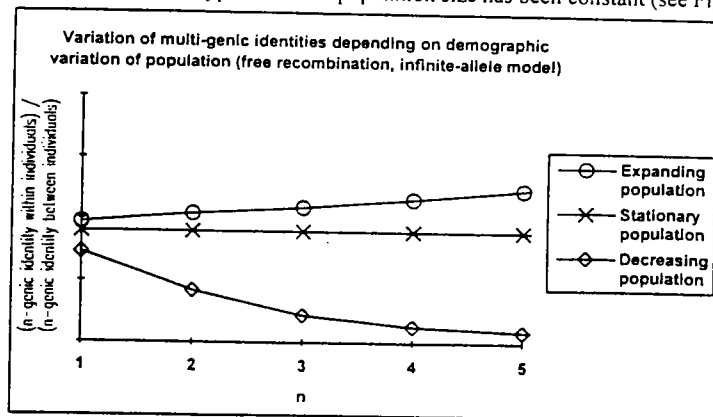
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Analyses of allele frequencies at different scales (within individuals to between populations) provides information about the reproductive system of the species, as well as the temporal and spatial structure of populations. F-statistics, that compute the average of 'gene identities' (i.e. probability of identity by state) at these different scales provide a synthetic account of the distribution of genetic diversity (i.e. Crow and Aoki, 1984, PNAS).

This approach can be generalized, considering multigenic identities between individuals I and J for n loci, where f_{IJ}^n can be defined as the probability that n randomly chosen genes from I and J are identical by state.

Analytical formulas for digenic identities, within individuals and between individuals' with populations, of order 2 (and approximations for higher orders), were obtained in the case of the 'Island Model' for different reproductive systems (selfing, parthenogenesis, random outcrossing), and 'k-allele model' (i.e. monogenetic identity between populations is $1/k$, k being the number of alleles). See Whitlock (1994, Evolution) for digenic identities, for the case of panmixia, 'infinite-allele' model. There is an exact correspondence of digenic identities with linkage disequilibria, partitioned in a within population component and a between populations components (see Ohta, 1982, Genetics).

Measures of these identities allow estimation of the model parameters (such as local population size and migration rate). They also allow testing some assumptions of the metapopulation model use (here the 'Island Model'), provided the number of measures is higher than the number of parameters. One can for example test the hypothesis that population size has been constant (see Figure).



Strong directional, and to some degree stabilizing selection, usually erodes only additive genetic variance while not affecting dominance variance. Consequently, traits closely associated with fitness should exhibit high levels of dominance variance. For this study a large number of estimates of dominance variance were compiled to determine if traits that are subject to strong selection and/or are closely associated with fitness have higher levels of dominance variance than traits less subject to selection pressure. Estimates were taken from the literature for both wild and domestic species and each group was treated separately. Traits closely associated with fitness (life history) had significantly higher dominance components than did traits more distantly related to fitness (morphology) for wild species. In addition, dominance variance was on average higher than additive variance for wild out-bred, life history traits. No significant differences were found between life history and morphological traits for domestic species. Traits that were known to have been subject to intense directional selection (morphological traits for domestic species) had significantly higher dominance estimates than did traits that were assumed to not have been subject to strong selection (morphological traits for wild out-bred species). The results are discussed with respect to the maintenance of heritable variation and the bias introduced in the calculation of the full-sib heritability estimate by high levels of dominance variance.

Dominance variance: associations with selection and fitness
Crnokrak P & Roff DA

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Molecular phylogeny of the *Myrmecia pilosula* group, including ants with the lowest (possible) chromosome number T

76 Australian ants of the *Myrmecia pilosula* species complex include some individuals (in *M. croslandi*) with the lowest possible metazoan chromosome number of $2n = 2$. Others in this cluster of sibling species have much higher numbers, the known maximum being $2n = 32$. Two species (*M. pilosula* and *M. 'banksi'*) are believed on cytogenetic and morphological grounds to have hybridized over a long period. To investigate the phylogeny and age of this group relative to the congeneric outgroup species *M. gulosa* we sequenced part of the cytochrome *b* gene and the intergenic sequence between it and a primer anchored on the nearby tRNA^{Ser}_{UCN} gene, and analysed the coding region using bootstrapped parsimony and NJ trees using the numbers of synonymous and non-synonymous codons per site. The intergenic space demonstrated a profusion of repeated sequences and only very closely related sequences (as judged by that for cytochrome *b*) showed detectable similarity at this almost 100% A+T region. In agreement with predictions from karyotype studies, the phylogenetic analyses showed that *M. croslandi* is the sister group to the other siblings; the time of separation of *M. croslandi* from the rest of the *pilosula* group is unexpectedly ancient. The comparisons between this group and an outgroup species, *Myrmecia gulosa*, allow an estimate of the evolutionary rate.

Crozier RH, Dobric N, Imai HT, Graur D, Cournuet J-M & Taylor RW T

**Preliminary Results on the Phylogeny and Biogeography of the Genus *Ilex*
(Aquifoliaceae)**

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The genus *Ilex* L. comprises some 400 species in five subgenera, the majority of which inhabit S.E. Asia and South America. Some species are also found in North America, New Caledonia, and the central Pacific Islands. Only 2-3 species occur in Europe, 1-2 in Australia and two in Africa. This disjunct pattern of distribution may be the result of extinction in Africa, Australia and central Eurasia. The genus is thought to be ancient, with fossil pollen dating from the Turonian (100-90 m. y. BP). Its extant representatives should thus reflect interesting biogeographical patterns through their phylogeny.

The genus is being investigated using comparisons of the chloroplast *atpB-rbcL* spacer and of the nuclear ribosomal internal transcribed spacer 1 (ITS1). The *rbcL* gene is also investigated but to a lesser extent. Rates of evolution of the different DNA sequences are compared. The phylogenies inferred from the different DNA sequences and their implications in the structure of the genus and in biogeographical questions are discussed.

18. **Replicable *in vitro* DNA Sequence Evolution of Bacteriophage T7** T
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Rapidly evolving viral genomes allow us to approach the ideal of actually observing the course of molecular evolution. We have achieved up to 7% DNA sequence divergence by growing lineages of bacteriophage T7 in the presence of the mutagen nitrosoguanidine. In the course of propagating independent T7 lineages we have observed two major classes of convergence at the DNA sequence level:

- 1) Formation of identical hybrid genes in replicated lineages; and
- 2) Repeated appearance and spread of the same 3 amino-acid substitutions.

Deletions of non-essential genes in the T7 genome can cause the fusion of the 5' portion of the 0.3 gene, which inactivates host restriction enzymes; and the 3' portion of the 0.7 gene, which produces a protein kinase. While the function of the 0.7 gene is compensated by genes appearing later in the life cycle, the 0.3 gene appears to maintain its primary function in all lineages we have observed. While 12 independent lineages, many stop codons appeared in the 0.7 gene, no stop codons appeared in the 0.3 portion of the hybrid gene. Furthermore, stop codons appear in the 0.7 portion of the gene at a greater frequency than one would expect by chance. This is consistent with a hypothesis that selection is acting to truncate the translated region of the hybrid gene. These combinations of deletions and mutations have resulted in hybrid genes -- of exactly the same length in translated amino acids -- in entirely independent lineages. Had we not observed the course of these events, we might have assumed that the chance of producing identical versions of these curious hybrid genes would have been very low. This might introduce a note of caution for systematists who give extra weight to deletions.

The previous set of lineages were each bottlenecked to a single individual every 50 lytic cycles to record the ancestral condition at each bottleneck. Naturally this bottlenecking introduces a strong element of drift. By propagating lineages *without* bottlenecking, we were able to generate strong selection for rapid lysis. The effects of selection were evidenced by a sharp decrease in time-to-lysis. Two of the genes we sequenced are considered "essential" genes, the 17.0 (tail fiber gene) and 17.5 (associated with lysis). In these genes, 9 amino acid substitutions appeared in samples taken at 100 lytic cycles, 3 of which went on to be "fixed" in a sample taken at 500 lytic cycles. This is a trajectory which we might expect from substitutions under positive Darwinian selection. But we need to know if this course of events will appear predictably. We found that 3 of the 4 mutations which had appeared early and become fixed in the first lineage had already appeared by 100 cycles in a second lineage. Even more intriguing is the observations that these 3 mutations appeared *together* in 2 of 10 individuals, and in no others. This replicated evolution is consistent with the idea that these three substitutions may be a favored genotyp

POLLEN HETEROMORPHISM, FLOWER MORPHOLOGY AND POLLINATOR BEHAVIOUR: A CORRELATION.

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In many species of modern angiosperms, each plant produces several pollen morphs that differ in their aperture number (the aperture is the only point of the pollen wall where the pollen tube can be initiated) : this phenomenon is called pollen heteromorphism. In several species of the genus *Viola*, all the plants observed have 3, 4, 5 and sometimes 6-aperturate pollen grains. Experimental results have shown that the more apertures a pollen grain has, the more quickly it germinates, but, on the other hand, the shorter its life-expectancy is. Theoretical models have shown that the production of several pollen morphs by the same plant is an evolutionary stable strategy. Furthermore, these models have suggested that some traits of pollination ecology (such as the attractiveness of flowers to pollinators and the frequency of their visits to the flowers) can affect the proportions of the different pollen morphs: the more frequent the pollinator visits are, the higher the proportions of many-aperturate pollen grains should be.

We experimentally test these predictions on several heteromorphic species of *Viola*. Our results show that:

- Within the genus, there is a negative correlation between the elevation at which plants were collected and mean aperture number. This is in agreement with the predictions of the model: as altitude increases, pollinators become scarcer and pollen waits longer to be transported to a receptive stigma, resulting in a higher proportion of few-aperturate/longer-lived pollen grains
- Within each species, there is a positive correlation between parameters of flower or spur size, and mean aperture number. This is again in agreement with our hypothesis as the most attractive flowers are also the most visited by pollinators and thus produce the highest proportions of many-aperturate/fast germinating pollen grains.

Experiments are also carried out to test the validity of the correlation between flower morphology, nectar production, pollinator behaviour and mean aperture number. Our results should enable us to confirm that traits of floral morphology might be correlated with traits of pollen morphology and physiology.

DENSITY DEPENDENT GROWTH OF THE BARLEY POWDERY MILDEW FUNGUS: INFECTION EFFICIENCY AND SPORE PRODUCTION

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One of the observations in all ecological systems is the dependency of fitness components on density, and for the barley powdery mildew fungus (*Erysiphe graminis* f. sp. *hordei*, abbreviated *Egh*) several studies have shown effects of density on spore production and other fitness components. An important factor influencing the effect of density on *Egh* fitness components is the mechanism of host defence.

Mathematical models were constructed in order to characterise density dependency. Infection efficiency and spore production when the fungus were measured at different inoculum densities when the fungus was growing on barley varieties with different levels of resistance.

Infection efficiency decreased with increasing inoculum density, the parameters of the density dependent model could be estimated.

Colonies at high densities had a lower latency period and tended to produce spores earlier than colonies at low densities, and the potential reproductive value of colonies (the potential reproductive value of an individual which has reached the state of colony forming) at high densities tended to be higher than from colonies at low density.

We suggest that early spore production at high colony density in *Egh* is caused by insufficient capacity of the resistance mechanism to "control" disease development, when *Egh* is present at high densities. The exact mechanisms behind resistance are unknown, however, one could speculate that the host plant, either because of resource allocation strategies or self-intoxicating side effects, has an upper limit on the amount of "resistance" in a leaf, and that this upper limit is insufficient to "control" mildew a high density.

EVOLUTION OF REACTION NORMS IN DROSOPHILA : T II
RESULTS OF A COMPARATIVE APPROACH AMONG SPECIES

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Temperature is a major abiotic ecological and evolutionary factor, especially for ectothermic organisms. In *Drosophila*, a selective role of temperature is generally considered for explaining genetic latitudinal clines in various widespread species or the geographic distribution of different species. Since most species are polyvoltine, they are generally submitted to temperature seasonal variations, which result in important phenotypic changes. This plasticity can be analyzed by studying the norms of reaction, i.e. the shape of the response curves for various characters, such as body size, pigmentation, ovariole or bristle numbers. A first conclusion is that the norms are non-linear when the whole range of temperatures compatible with the development are considered. Mathematical adjustments are needed to describe the norm. A second conclusion is that the thermal range is much variable among species : for example 7-27°C for a temperate species and 16-31°C for a tropical one. The last conclusion is that significant and sometimes important differences may be observed in the shapes of the curves of various species. The direction of the variations strongly suggest their adaptive significance. Whether such changes are mediated by specific regulatory genes acting on the norms, remains however an open question.

EVOLUTIONARY CONSEQUENCES OF A TRADE-OFF BETWEEN PARENTAL
EFFORT AND MATING EFFORT.

I investigate the evolution of the roles of the sexes in a dioecious population. In particular, I consider how males and females partition their resources between parental effort and mating effort. Previous models have neglected the effect of evolutionary changes in the male and female strategies on the availability of mates.

I analyze a simple game theoretic model where competition for access to mates takes the form of aggressive contests between members of the same sex, the outcome of which depends on the mating effort of each participant. Three versions of this model are analyzed. In the simplest version, variation among individuals of each sex is allowed only in their total parental effort. In the more elaborate versions of the model, variation is also allowed in the parental investment per offspring. When this type of variation is allowed, the only pairs of male and female strategies that are stable with respect to invasion by initially rare mutant strategies are strategy pairs where only one sex contributes parental effort. However, when non-heritable variation in the resources available to individuals is introduced (the third version of the model), it is found that parental effort by both sexes can be maintained.

Genotypic demography: simultaneous dynamics of numbers and allele frequencies.

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A population can be characterized by its numbers and by its level of genetic variation. In a population with discrete generations a locus with two alleles is present: as a consequence, three genotypes exist. The numerical dynamics of the population are determined by the numbers of these three genotypes born at each time unit. The three quantities, - the numbers of the three genotypes -, can be rearranged to yield the simultaneous dynamics of numbers n , allele frequency p and deviation from Hardy-Weinberg frequencies F . By standard linearizing around the simultaneous equilibrium n^* , p^* and F^* , the dynamical behaviour of the system can be described.

1 The first question is when the dynamics of n , p and F are decoupled, i.e., when a separate description of numerical dynamics is sufficient to account for the dynamical behaviour of number, and a separate description of allele frequency dynamics is sufficient to account for the dynamical behaviour of allele frequency.

If number and allele frequency are dynamically coupled and a separate description of the total dynamics is not sufficient, the following questions arise next:

2 The second question is whether numerical stability is determined in exactly the same way in a population with three genotypes as in a population with one genotype.

3 The third question is about the influence of mating structure on the dynamics of a population. Interaction in the mating structure or different selection in males and females can lead to deviations from Hardy-Weinberg proportions. These deviations form part of the dynamical system of the populations, and can contribute to numerical fluctuations.

THE MAINTENANCE OF MALE STERILITY.

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Anita A. de Haan, Jos M.M. van Damme.

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Netherlands institute of Ecological Research (N.I.O.O.-C.T.O.)

Populations of *Plantago lanceolata* (ribwort plantain) consist of individuals which are hermaphrodites (male and female expression: H) and individuals which are male sterile (only female expression: MS). The sexual system is called GYNODIOECY.

Both phenotypes H and MS are the result of an interaction of cytoplasmic genes and nuclear genes. Cytoplasmic genes (CMS types) are transmitted to the progeny only by ovules, while nuclear genes are transmitted by both ovules and pollen. A CMS type which is transmitted only by ovules can spread in a population even if it only has a small fitness advantage in f.e. seedset. It is therefore necessary to take into account the mode of inheritance for an explanation of the occurrence of male steriles.

The nuclear restorer genes are transmitted both by ovules and pollen. The question is: "If restorers occur in a population how are the male steriles maintained?" Two alternative hypotheses are possible. Either new CMS types arise repeatedly by mutation, or only a limited number of CMS types exists and they are spread over populations by migration. In the second case the frequency of restorer alleles should not become fixed, because then no male steriles can occur. A way in which the frequency of restorers would stay low is if there are costs of restoration.

In the case of *P. lanceolata* four different CMS types are found, of which CMSI is the most frequent male sterile type in the field. By comparison of chloroplast variation of the four CMS types from a limited number of plants sampled worldwide, it seems most likely that the occurrence of CMSI is due to migration. Among CMSI types there is stronger relationship than among different CMS types of plants from one population.

While the results show that maintenance of male sterility is probably not due to mutation, no evidence is found for costs of restoration. Two experiments in which plants with and without restorer alleles are compared do not show significant differences in fitness in the assessed parameters under suboptimal conditions. It is possible that either the costs of restoration are very low, or under the given conditions they are not visible. If costs of restoration do not exist, there have to be other mechanisms which prevent the restorer alleles to go to fixation.

Diel vertical migration and size-dependent habitat partitioning in *Daphnia*: a tower experiment on the impact of fish predation on clonal coexistence

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Diel vertical migration among zooplankton is generally considered to be a strategy to reduce vulnerability to visually-orienting predators (e.g. fish); zooplankton reside at greater depths during the day, and migrate into the upper waters during the night. In the case of intrapopulational variability in body size, large individuals are expected to migrate to greater depths than small individuals. We conducted an experiment in large (11.5 m x 0.8 m) indoor plankton towers. Three genetically distinct clones of *Daphnia hyalina x galeata* were stocked in equal densities into each of the towers. The clones were isolated from the same lake (Schönsee, Germany), and were characterized by differences in body size. Significant clonal differences were observed in daytime vertical distributions, with the largest clone residing at a greater depth. Importantly, two of the three clones, which showed contrasting body sizes, were characterized by a very similar relationship between average body size and depth among the adults. The results of a selection experiment in which mixed populations of the three clones were subjected to predation by fish indicated that the two aforesaid clones exhibited essentially the same relative fitness in the presence of visual predators. This was irrespective of the large differences in body size and vertical migration behaviour. It is our hypothesis that the differences in body size and day-depth are associated in such a way that the effects on vulnerability to visual predators of each of the single traits are balanced. Our results suggest that a complex association between behavioural (i.e. habitat selection) traits and life history strategies may underlie intrapopulational genetic polymorphism in vertical migration in zooplankton, via a balancing of fitness effects.

Deleterious mutations and the ecology of sex in
Chlamydomonas.

De Visser, J.A.G.M. (Arjan)*, Rolf F. Hoekstra & Herman van den Ende (Dept. of Genetics, Wageningen Agricultural University; Dept. of Molecular Cell Biology, University of Amsterdam, The Netherlands)

Theoretically, one of the most general benefits of sex is given by its more efficient elimination of deleterious mutations. This theoretical advantage of sex is deterministic if deleterious mutations affect individual fitness in a synergistic way. Here, we present a new test for synergistic epistasis by considering the skewness of the fitness distribution of sexually produced offspring of two parents. We crossed two strains of the haploid, unicellular alga *Chlamydomonas eugametos* and used the logistic parameters r and K of each offspring's clonal growth rate as measures of fitness. In a second cross, UV was used to cause additional deleterious mutations in the parental strains. The results indicate that mutations affecting the carrying capacity (K) interact in a synergistic way, while mutations affecting the maximum growth rate (r) show independent effects. These results suggest an alternative explanation of the general observation that sex is related to constant, undisturbed environments (K -selected), while asexual reproduction is found in more variable environments (r -selected). A mechanistic explanation for the differential interaction between deleterious mutations on K and r is sought in the underlying metabolism.

The dynamics of mitochondrial plasmids in a Hawaiian population of *Neurospora intermedia*.

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Generally mitochondrial plasmids in fungi seem to be stable both mitotically and meiotically. In crosses these plasmids are maternally transmitted as is generally the case for cytoplasmic elements. However, exceptions to the general rule of strict and efficient maternal inheritance have been found in *Neurospora*. On the other hand alternative modes of plasmid transfer have been observed in *Neurospora* too.

In this study we investigated the population dynamics of two different plasmids using a Hawaiian population as a model. The distribution of two mitochondrial plasmids among natural isolates of *N.intermedia* from Hawaii has been investigated. 74% of the isolates carried the neutral circular plasmid Han-2, whereas 38% contained the linear senescence causing plasmid kalDNA. The distributions of the two plasmids are independent and there is no significant difference between the population of 1972 and 1976.

In order to further examine the reasons for the observed frequency distribution we studied horizontal and vertical transmission modes of the plasmids.

ADAPTATION AND LOCAL MALADAPTATION IN MEDITERRANEAN BLUE TITS

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Blue Tits (*Parus caeruleus*) living in patchy Mediterranean landscapes show an extensive variation in life history traits. In these habitat mosaics the timing and abundance of food resources much differ depending on whether the dominant tree species in the habitat is summergreen (deciduous) or evergreen.

Some of these populations show evidence of local maladaptation. In mainland Southern France, laying date in evergreen habitats is too early in relation to the peak of food abundance, and reproductive success is low. The "source-sink hypothesis" predicts that between-habitat differences in the local production of fledglings should result in an asymmetrical gene flow from summergreen habitats ("source") to evergreen habitats ("sink") which prevents adaptation in the latter.

This hypothesis has been tested using different approaches.

Two habitat mosaics genetically isolated from each other were studied, one on the mainland and one on the island of Corsica.

Data were collected on tree phenology, food abundance (caterpillars), breeding traits, and morphometry of adults and offspring.

We demonstrated that within each mosaic landscape, laying date and clutch size are adapted to the habitat type where breeding success is higher (summergreen on the mainland, evergreen on Corsica). The number and quality of fledglings depends on the synchronisation between food availability and timing of reproduction. In adults, there are between-habitat differences in male body size, but not in females.

The distribution of genetic variability was analysed using single-locus minisatellite DNA probes. The results are consistent with predictions of the source-sink hypothesis: source and sink habitats are not genetically differentiated; the amount of gene flow between source and sink habitats is much higher than between source habitats or between sink habitats; linkage disequilibrium is higher in sinks than in sources. This supports the source-sink hypothesis and is consistent with results from the other approaches.

This study emphasizes the need of combining genetic and ecological studies to understand the functioning of spatially structured populations.

THE DYNAMICAL THEORY OF COEVOLUTION
--- A UNIFYING PERSPECTIVE

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A unifying framework is presented for describing the phenotypic coevolutionary dynamics of a general ecological community. We present an individual-based approach allowing for the interaction of an arbitrary number of species. The adaptive dynamics of species' trait values is derived from the underlying population dynamics within the community; in consequence, the evolutionary process is driven by ecological change.

We present a hierarchy of four dynamical models for the investigation of coevolutionary systems. The necessity of stochastic treatment is demonstrated and deterministic approximations are derived where appropriate. The mathematical framework advanced here to our knowledge is the first one to combine the individual-based, stochastic perspective with a fully dynamical analysis of the phenotypic coevolutionary process.

Deductions are given to derive various well-known equations from the literature of (co)evolutionary modelling as special cases of our approach. In particular, equations central to the fields of evolutionary game theory, adaptive dynamics, replicator dynamics and selection-diffusion systems are recovered. In doing so, several ad-hoc assumptions can be removed and the different domains of validity for these models can be delineated.

DIFFERENTIAL SELECTION ON X CHROMOSOME LOCI IN THE EUROPEAN HOUSE MOUSE HYBRID ZONE .

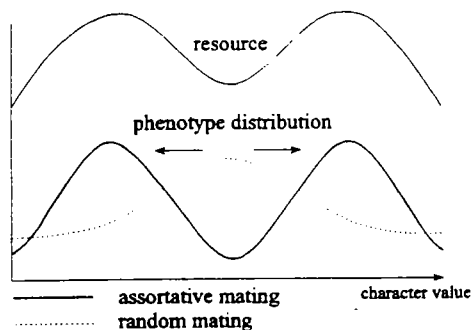
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Although it has often been assumed that tension zones are maintained by weak selection acting on many loci distributed throughout the genome, previous results suggest that only few gene systems come under selection in the hybrid zone between *Mus musculus domesticus* and *M. m. musculus*. The narrow clines obtained for sex chromosome markers suggested that one of the functions that is perturbed in the hybrid genomes is X chromosome function. The selective pressure on different regions of the X chromosome has been investigated by analysing the clines obtained with a series of microsatellite markers. The differences in cline widths suggest that gene systems on the proximal region of this chromosome are more strongly selected against than those towards the distal end.

I present a model in which a founder population encountering a bimodal resource distribution splits into two reproductively isolated subpopulations due to frequency-dependent selection. In the model, the phenotype of an individual is given by the value of a quantitative character such as size. The fitness of a phenotype depends on the available resources and on the frequency distribution of all phenotypes. In each generation, this distribution first changes according to the selection regime. Then mating determines the distribution at the beginning of the next generation. The corresponding genetics are modeled explicitly with many loci that determine the phenotype additively. This allows to model assortative mating, in which matings between individuals of similar phenotypes have a higher frequency than with random mating. If the resource distribution is unimodal, so is the equilibrium distribution of the phenotypes, and no reproductive isolation occurs. However, if the resource distribution is bimodal, an initially unimodal phenotype distribution also becomes bimodal (see Figure), with very little matings taking place between the two subpopulations given by the two humps in the distribution. Thus a bimodal resource distribution leads to reproductive separation. This does not happen when mating is random, in

which case the phenotype distribution remains unimodal. Since there must be some clue for recognition between mating partners, some degree of assortative mating between similar phenotypes is realistic. The model shows that this, together with frequency-dependent selection, can lead to reproductively isolated populations whose phenotype distributions have very little overlap, each population matching one mode of the bimodal resource distribution. The evolution of the degree of assortative mating can also be studied by introducing a modifier locus.



Since two reproductively isolated subpopulations can match a bimodal resource distribution better than one unimodal population, assortative mating is favoured, which in turn leads to speciation by the mechanism described.

TIG/19

The evolution of phally polymorphism
in the hermaphrodite freshwater snail *Bulinus truncatus* :
genetic variation of the aphyally frequency within and between populations

Doums C., B. Delay & P. Jarne

The evolution of sexual polymorphisms, such as gynodioecy in plants, provide an excellent opportunity to study the evolution of selfing since the ratio of the sexual morphs directly influence the rate of selfing in a population. Some species of self-fertile hermaphrodite gastropods are characterized by the co-occurrence of two sexual morphs in natural populations : regular hermaphrodite called euphallic individuals and individuals which are deprived of their male copulatory organ called aphyallic individuals. The two sexual morphs can reproduce by selfing. However, when outcrossing, aphyallic individuals can only play the female role since they can not transmit sperm to other snails. The selfing rate in a population must therefore increase with the aphyally ratio since in strictly aphyallic populations, selfing is obligatory.

This singular sexual polymorphism is therefore an excellent model for the study of the evolution of selfing and sexual polymorphisms, provide that aphyally is at least partly genetically determined and that there is some genetic variation of the frequency of aphyally individuals in natural populations. First, even if environmental factors (temperature) play a role in the determination of the sexual morphs, we show that aphyally is largely genetically determined. An individual, whatever its sexual morph, can be characterized by the frequency of aphyallic individuals among their offspring. Second, we investigate the magnitude of the genetic variability of the character 'frequency of aphyallic offspring' among and within natural populations, using about 550 individuals originated from 15 natural populations. For six populations, we estimate the genetic variability within populations over time.

A high level of genetic variability was observed between populations and within some populations. This result is discussed both in relation with the population dynamics of these snails and with the different selective factors which can act on the evolution of aphyally.

4 Chromosomal, molecular and reproductive evidence for the presence of two distinct species of *Arvicanthis* (Rodentia: Muridae) in West Africa

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Rodents of the genus *Arvicanthis* are morphologically very similar throughout their West African distribution, and have thus been conventionally referred to the sole species *A. niloticus*. However, our preliminary karyotypic and electrophoretic results were supporting a polytypic structure for the species.

In the present investigation, R- and C- band chromosome patterns have been prepared for 15 individuals from 5 different countries (Mauritania, Senegal, Mali, Burkina-Faso and Niger) and show unequivocally the existence of two distinct karyomorphs, differing from each other by numerous rearrangements such as pericentric inversions and reciprocal translocations as well as differences in constitutive heterochromatin quantity. The level of overall genetic divergence between these karyomorphs was also examined with DNA/DNA hybridization experiments and proved to be of a specific level, whereas crosses between the two morphs failed to produce offsprings. We conclude from this body of data that both karyomorphs correspond to good biological species and deserve taxonomic naming. This represents another case of sibling species of African rodents which raises the problem of the evolutionary processes involved in the speciation event. The two species appear to be parapatrically distributed, their distribution areas corresponding to the sahelian and sudanian domains respectively.

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Polyploidy and clonal diversity in an arctic cladoceran.

Genome size determinations were coupled with allozyme and mtDNA studies to gain insights into the origin of polyploidy and clonal diversity in populations of *Daphnia tenebrosa* from Churchill, Manitoba. Allozymic variation at 5 enzyme loci allowed the detection of thirty two clones. Analyses of 73 populations in 1981, 27 in 1987, and 45 in 1991 revealed that clonal frequencies were relatively stable and that *D. tenebrosa* was more clonally diverse (average of 3 clones per pond) than other species of the *D. pulex* complex at the same site. Genome size determinations revealed the presence of two clonal assemblages with averages of 0.53 (± 0.01) pg and 0.89 (± 0.03) pg, corresponding to diploid and tetraploid clones. Clustering of allozyme distances revealed three groups, with no association between ploidy level or pigmentation. Similarly, diploid and polyploid clones did not form distinct clusters on the mtDNA dendogram. The high sequence divergence between the two mtDNA clusters as well as the lack of correspondence between allozyme distance and mtDNA divergence among clonal pairs both suggest that polyploidy arose following reciprocal hybridizations between genetically divergent populations of this species.

STRATEGIES OF TRANSOVARIAL TRANSMISSION BY A MICROSPORIDIAN SEX RATIO DISTORTER IN *GAMMARUS DUEBENI*.

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Populations of the crustacean *Gammarus duebeni* are infected with a microsporidian sex ratio distorter. The parasite is transovarially transmitted to the offspring of infected mothers; and infected young are feminized by the parasite. Males do not transmit the infection. Parasitic sex ratio distortion increases the rate of parasite transmission to the next host generation.

We investigate the strategy of transovarial transmission of the microsporidian parasite of *G. duebeni*. Vertically transmitted parasites must overcome two bottlenecks to ensure infection of future host generations: transmission from adult to egg; and transmission to the germ-line of the infected host. We find that transmission of the microsporidian from adult to eggs is highly efficient, whereas transmission within infected embryos to the germ-line is relatively inefficient. We measure parasite distribution between cells of developing embryos and use these distributions to infer possible mechanisms of transmission to the germ-line. Parasite distribution within the embryo appears to be dependent on host cell lineage, and is not consistent with unbiased segregation between daughter cells. This indicates that the parasite segregate together at host cell division and may reflect a strategy of differential segregation to the germ-line.

**The choice of DNA sequence for taxonomic studies of planthoppers
(Homoptera: Delphacidae)**

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Different regions of the ribosomal DNA genes evolve at different rates, and are suitable for study for different taxonomic levels. However, to a certain extent the rate of divergence also depends upon the group of organisms being studied. Similar principles will apply to other parts of the genome. Therefore the taxonomic suitability of particular gene sequences has to be confirmed for the different taxa.

Analysis of genetic diversity and clonal spread in discrete populations
98 of aspen (*Populus tremula* L.) using isozyme analysis. T5?
ric Easton. Institute of Ecology and Resource Management, Darwin Building, Kings Buildings.

Mayfield Road, Edinburgh.

The growing interest in native woodlands in Scotland has exposed large gaps in our knowledge of its indigenous species. One such species is Aspen (*Populus tremula* L.). Aspen is widely distributed throughout Scotland but is usually found at low population density as single trees or small monoclonal stands except in Strathspey and Deeside where it can be found in woodlands up to 40 ha. These woodlands are unique in Britain with a total area of only 175 ha., moreover, they support a rare and threatened insect assemblage. Consequently they are considered to have high conservation value and there is pressure to include aspen in the many schemes to establish new native woodlands.

Aspen, however, produces seed very rarely in Scotland and almost all regeneration is believed to originate from root suckers. This has led to the assumption that large stands of aspen are monoclonal or have very few clones within them. As most of the available planting stock is derived from root cuttings it is important to adequately measure genetic diversity in natural woodlands to allow prudent collection and deployment of the planting stock in the creation of new native aspen woodlands.

This paper will outline two studies where isozyme markers were used to evaluate the variation present in two discrete populations of aspen. Both studies used five variable isozyme systems developed from previous population structure work for the identification of genotype. Whilst exploiting a much lower level of variation than RAPDs, isozyme analysis proved a quick, cheap and accurate alternative to the more hip RAPD technology and was more appropriate to the limited variability expected in this species.

The first study is a base-line survey of variation within a single natural aspen woodland. Two hundred trees were sampled from within a six ha. subsample and their genotype determined using isozyme analysis. The position of the trees was mapped and the genotypes plotted providing data on the number of clones present within a native woodland and how these clones are distributed within the wood. From the results management guidelines can be drawn up for the establishment of new native aspen woodlands and the collection of root material for the propagation of new planting stock.

The second study is a case-study showing the use of isozyme analysis in the estimation of genetic variation within the small aspen population on Orkney. There is a desire to establish new native aspen woodlands on Orkney using, as far as possible, Orkney-derived planting stock. The aim was to determine the number of clones on the islands and their position. From the results it was possible to evaluate whether there was enough variation present to allow the use of only Orkney aspen in planting schemes and to draw up guidelines for the collection of root material for propagation of planting stock and the establishment of new aspen woods optimising the available genetic variation.

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IT1

Ebert, D. The co-evolution of virulence. NERC Centre for Population Biology, Imperial College at Silwood Park, Ascot SL5 7PY, England

The concept of reciprocal selection underlies host-parasite co-evolutionary arms races. Its driving force is the reduction of host life span or fecundity that is caused by a parasite. Parasites evolve to optimize host exploitation, while hosts evolve to minimize the parasite induced loss of fitness. Research on the evolution of virulence has mostly emphasized the role of parasite evolution in determining virulence. However, host evolution, accelerated by sexual recombination, contributes to the evolution and expression of virulence as well. Genetic variation among hosts selects for reduced virulence. I outline a synthesis between current thinking about the evolution of virulence and the evolution of sex. This leads to experimentally testable hypotheses on the Red Queen hypothesis and the co-evolution of virulence. I use examples from my work on *Daphnia magna* and some of its microparasites to support these hypotheses.

TESTING THE ROLE OF DEVELOPMENT IN EVOLUTIONARY RADIATIONS

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T15

Most modern discussions of major evolutionary radiations have been framed in terms of development, ecology, or both. One must acknowledge that all organisms develop and have an ecology at the same time, and that many times paleontological data are bound to be consistent with more than one hypothesis. Answers are not likely to come in simple form; they depend on the specificity of the questions, the nature of the data and the definitional status of key concepts like "developmental constraints".

(1) The specificity of the questions. Understanding of the causal nexus underlying radiations has to go beyond consistency arguments. I suggest that the role of development can be better tested explicitly, by direct inclusion of developmental information or its proxies in comparative and temporal studies. I review some previous tests relating to fluctuating asymmetry, character correlation and non-adaptations, and outline a few new ones -- involving temporal comparisons of developmental and adult morphospaces, of theoretical and empirical morphospaces, and the study of radiologies.

(2) The nature of the data. Taxonomic data have been traditionally used as proxies for morphological distinctness, and many evolutionary radiations have been described in these terms. Some explanatory hypotheses, like Sepkoski's null hypothesis of exponential diversification and Kauffman's rugged fitness landscapes model, are amenable to the use of taxonomic data, and I provide explicit tests of such hypotheses. However, direct studies of morphological disparity and the construction of morphospaces are sine qua non for further understanding of evolutionary radiations.

(3) Definitional standardization. With the growing solidification of evolutionary developmental biology comes the need for mutual agreement on its key concepts. "Developmental constraint" is perhaps the most important in this regard. I provide a brief yet rigorous analysis of the concept, expand its realm of applicability, and argue that its contribution to the understanding of failure to radiate can be instrumental in the study of the role of development in evolutionary radiations.

Life history evolution in *Asobara tabida*

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One of the most important principles in life history theory is the existence of trade-offs, such as the cost of reproduction. Natural selection will favor that combination of traits which will maximise fitness. In different environments the optimum of the trade-off may vary. *Asobara tabida* is a solitary parasitoid which occurs throughout Europe. It experiences different ecological conditions in northern and southern Europe. In northern Europe breeding opportunities are rare and the travel times between patches may be long. In southern Europe breeding sites are more abundant. The differences in habitat may influence the life history parameters and the optimum of the trade-off between reproduction and longevity.

Allocation to reproduction (number of eggs in the ovaries) and to survival (amount of fat) differed between strains: northern strains have a greater amount of fat, while southern strains have more eggs. Northern strains live longer than southern strains, which confirms that longevity is correlated with the amount of fat. When parasitoids were allowed to reproduce every day, longevity decreased in both northern and southern strains, so there is a cost of reproduction. Southern strains have a high reproduction early in life, while northern strains produce a lower number of offspring per day but continue longer with the reproduction. Allocation to fat and eggs is not a fixed: *A. tabida* can replenish its egg supply after oviposition at the cost of its fat reserves. There is no resorption of eggs. These results show that it is possible to 'switch' from fat to eggs, but not the other way around.

This implies that there is not only adaptation to the MEAN richness of the environment by a difference in allocation, but there is also adaptation to the VARIANCE in richness of the environment. By having a large eggload at an early age the southern wasps lose part of their flexibility, but gain time in reproducing. Being in a relatively predictable environment with selection on early reproduction this is probably the best strategy. In the north however, the time spent searching for breeding sites is more variable. By postponing the moment they use fat reserves to make eggs northern parasitoids have a greater plasticity to adapt to the environment.

Phenotypic Variation in Plant Resistance - Implications for Pathogen Evolution

R. A. Ennos & K. C. McConnell, IERM, University of Edinburgh

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The resistance of a plant to a pathogen may be defined very generally as the relative ability of that plant to prevent a pathogen induced reduction in its fitness. Variation in resistance among plants may occur if there are differences in the probability of pathogen dispersal to infection sites, if there are differences in the probability of pathogen establishment on plants, and if there is variation in the rate and extent of development of the established pathogen on the plant. Thus resistance variation may have a multiplicity of causes in natural populations, and be due to variation in a diversity of attributes. For these reasons caution needs to be exercised in defining and making general statements about 'costs' of resistance.

To understand the evolution of plant resistance, all forms of resistance variation need to be considered jointly so that their relative impact on the fitness of host plants in natural populations can be assessed. A preoccupation with ideas derived from agricultural crop systems has led to an overemphasis on the importance of selection which alters the probability of pathogen establishment, and a neglect of studies looking at selection for resistance expressed through pathogen avoidance and reduction in the speed and extent of pathogen development on the host plant.

Resistance to pathogens is an aspect of plant phenotype, and is affected not only by plant genotype, but also by environmentally induced variation. In many natural situations, environmental effects on plant resistance will be far greater in magnitude than genetic effects. It may not be necessary to seek a selective explanation for much of the genetic variation in resistance that has been reported, especially if estimates of the selective impact of genetic variation for resistance have been exaggerated as a consequence of measurement under novel and uniform environmental conditions.

The fact that variation in plant resistance may have a substantial environmental component must be integrated into our understanding of pathogen evolution. To do this, information is required on the response of pathogen populations to selection on hosts showing environmentally induced variation in resistance. In natural plant populations, resistance to many necrotrophic fungal pathogens shows substantial environmentally induced variation. Plants growing under stress tend to show lower resistance than unstressed plants. We have conducted experiments with genetically marked fungal isolates to determine whether the relative fitness of genotypes of the ascomycete *Crumenulopsis sororia* varies with the degree of environmentally induced stress in their pine host. The results of these experiments and their implications for pathogen evolution will be discussed.

The systematics of the New Zealand flightless beetle genus *Prodontria* with some biogeographic and conservation implications

B.C. Emerson and G.P. Wallis

The beetle genus *Prodontria* is of importance to New Zealand conservation programs. All *Prodontria* species are brachypterous (having reduced wings), and the genus presents some interesting evolutionary and biogeographic questions that are testable using phylogenetic reconstruction. A phylogeny was produced for 14 flightless *Prodontria* species, two macropterous (fully-winged) *Odontria* species and single representatives of two outgroup genera, using sequence data from the mitochondrial COII gene. The data support probable conspecificity of the morphologically similar *P. modesta* and *P. bicolorata* but do not support their hypothesised sister species relationship with the geographically proximate *P. lewisi*. The alpine *P. capito* is found to be a paraphyletic group with the most eastern population diverging after the western populations made their appearance. Many interesting biogeographic disjunctions are here proposed to be anomalous and the result of morphological convergence. The data do not support the idea of a common flightless ancestor for *Prodontria*, but suggest that brachyptery has evolved numerous times. In some instances, this appears to have led to contemporaneous speciation resulting in little resolution of phylogenetic relationships in some parts of the tree. These data allow for a new interpretation of the origin and diversification of the southern New Zealand flightless melolonthine fauna. Multiple speciation events involving wing reduction are suggested to involve at least one widespread flighted ancestor that has given rise to brachypterous forms.

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THE END-PERMIAN MASS EXTINCTION: WHAT DIFFERENCE DID IT MAKE?

The end-Permian mass extinction was the most extensive of the Phanerozoic, and perhaps in the history of life. Over an interval of 1-3 million years some 80-95% of all skeletonized marine species became extinct. On land, severe extinctions occurred among tetrapods and insects: recent work has produced considerable evidence for sudden ecological changes among plants, although little evidence for mass extinctions. The marine faunas of the Palaeozoic were dominated by epifaunal, sessile, filter-feeding clades, but following the extinction, the clades which came to prominence included many more burrowers, infauna and predators. John Phillips recognized the fundamental nature of this interval for the history of life in 1841, and used it to define the end of the Palaeozoic Era and the beginning of the Mesozoic Era. Data from marine gastropods demonstrates considerable biogeographic structure to the extinction: the early phase involved extinction of endemic genera as marine basins dried out. Later, most endemic genera had disappeared and widespread genera were eliminated. This data also indicates regional differences in the pace of extinction. Unlike every other mass extinction, recovery was delayed for some 5 million years, evidently because of the breadth of ecological disruption rather than continuing harsh environmental conditions.

The past few years have seen an explosion of knowledge about the end-Permian mass extinction, including detailed paleontological and geochemical studies and detailed analyses of the physical events which span the interval. These studies demonstrate that the extinction occurred during a period of rapid changes in the physical environment, including rapid changes in sea-level, apparent oceanic anoxia, extensive volcanism (including the eruption of the Siberian flood basalt, the most extensive continental flood basalt of the past 600 million years) and changes in ocean chemistry. Together the fossil record and the physical events suggest that the unprecedented magnitude of this extinction reflects not a single cause, but rather a series of events.

In contrast to sudden, catastrophic extinctions, termed pulse events, the end-Permian event seems to have been a more protracted press extinction. The length of press extinctions allows adaptation, at least in some groups. Thus patterns of survival and recovery may be very different between the two types of mass extinction.

Curiously, uncertainty remains over the long-term importance of the end-Permian mass extinction. Sepkoski has argued that the expansion of groups which dominate the post-Palaeozoic began hundreds of millions of years before the end-Permian, and thus that the mass extinction merely accelerated trends already established. In contrast, other data suggests that the structure of modern marine communities largely reflects patterns of extinction and survival during the extinction.

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THE DEVELOPMENTAL EVOLUTION OF METAZOAN BODY PLANS: THE FOSSIL EVIDENCE

The rapid origination of higher metazoan bodyplans during the late Neoproterozoic and early Cambrian (580-530 million years ago) was intimately associated with innovations in developmental control mechanisms. Evidence for many of these innovations are preserved in the fossil record, and a synthesis of evidence from developmental biology, the fossil record and metazoan phylogeny allows for tests of the relationship between developmental innovation and the explosion of bodyplans. Significantly, many of the developmental control mechanisms are broadly distributed among metazoa and appear to have been in place well before the Cambrian radiation of bodyplans. Thus, the radiation may represent the achievement of a threshold in the complexity of developmental controls.

The evolution of the Hox gene cluster provides perhaps the best example of the diversification of these control mechanisms in association with the appearance of increasingly complex morphologies. While there is no on-to-one correspondence between morphological complexity and the size of the cluster, there is evidence that minimum levels of complexity within the Hox cluster were required before complex morphologies could evolve. Of critical importance to unraveling the association between the evolution of the Hox cluster and major metazoan body plans are: 1) the date of the protostome/deuterostome divergence; 2) the date of the origin of the novel body plans (which, of course, is unlikely to coincide with the clade divergence based on molecular evidence); and 3) the pattern of increase in complexity of the Hox cluster. **The Fossil Record.** No demonstrably coelomic organisms have been described from the late Neoproterozoic soft-bodied Ediacaran Fauna, and the highest level of morphologic complexity documented by trace fossils of this interval could have been produced by actively burrowing 'worms' with a hemocoelic grade of organization. Although true protostomes or deuterostomes may have been present at this time, no firm evidence for this level of complexity has been advanced. The earliest undisputed bilaterian fossils appear during the early Lower Cambrian, about 535 mya, and can unambiguously be assigned to protostome clades. **The evolution of the Hox cluster:** Considerable information is available for some groups, but reliance on PCR surveys for annelids, molluscs, and some arthropods has hindered the development of unambiguous evidence of cluster evolution. The models presented during this talk do provide a testable framework for future work by paleontologists and developmental biologists.

Genetics of incipient speciation in *Drosophila mojavensis*: the role of epicuticular hydrocarbons.

Geographically isolated populations of cactophilic *Drosophila mojavensis* from mainland Mexico and the Baja California peninsula exhibit low, but significant premating isolation in laboratory mate choice trials. This system has been the subject of over 20 years of study due to the importance of understanding the initial stages of reproductive isolation or incipient speciation. The role of epicuticular hydrocarbon (EHC) variation, particularly sexual dimorphism in the relative amounts of C_{35} and C_{37} alkadienes, has been implicated in patterns of mate choice, but little information exists about such variation in wild flies. The influences of larval substrates on adult mating behavior has been documented: fermenting cactus tissues decrease the magnitude of premating isolation as compared with artificial substrates. In order to assess the effects of such larval substrates and genetic determinants on EHC variation, EHC profiles were determined from flies that were the subject of a bi-directional artificial selection experiment on egg to adult development time using two populations of *D. mojavensis* reared on each of two host cacti. Premating isolation decreased uniformly in the lines selected for slow development time, in several of the fast lines, but not in the controls. Correlated responses in EHC composition in these selection lines will be discussed in relation to patterns of host use in nature and the origins of reproductive isolation.

This research was funded in part by NIH, NSF, and the University of Arkansas.

Patterns of Polyandry in the Leafcutter Ant *Atta colombica* - Microsatellite Genetic Data and Sperm Counts Compared.

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Polyandry in social insects is of considerable interest due to the consequences it has for relatedness and genetic diversity within colonies, factors which may affect both the inclusive and direct fitness of workers and queens, and the colony-level fitness, eg. via an increased resistance to pathogens. In general, effective queen-mating frequencies are low in the eusocial Hymenoptera. The advanced genus of leafcutter ants *Atta*, however, seems to contain species with remarkably different queen-mating frequencies (as estimated by sperm content analysis), ranging from 1 to 4. matings per average queen. This makes the genus an excellent choice for studying interspecific variation in the degree of polyandry and for investigating the life history correlates and genetical and sociobiological consequences of such variation. Moreover, the local ubiquity of *Atta* species in the Neotropics allows detailed intraspecific analyses of variation in queen mating frequency.

Data on male sperm content and queen spermathecal sperm content (Fjerdingstad & Boomsma, submitted) have shown that *Atta colombica* queens typically receive what corresponds to the sperm complement of one average male, suggesting a mean mating frequency of approximately 1. Data of this kind do not preclude the existence of higher effective queen-mating frequencies as it is generally unknown how much sperm is transferred per mating. With the purpose of analysing polyandry in various species of *Atta*, a partial genomic library of *Atta colombica* was created and screened for dinucleotide repeat microsatellites, and primers were designed for 3 loci. All 3 primer pairs were found to be locus-specific and to amplify not only in *A. colombica*, but also *A. sexdens*, and *A. cephalotes*. An analysis using these highly variable genetic markers was carried out on queens, and nestmate workers and males of the monogynous *A. colombica* and prove the existence of substantial levels of effective polyandry. A preliminary analysis based on a small subsample of workers showed that in 12 out of 26 colonies queens had mated twice or more. Further genetic analysis of larger numbers of workers is likely to reveal that polyandry is even more frequent in *Atta colombica*, contrasting with the provisional conclusion based on sperm count analysis. When combined, the genetical and the sperm count data also suggest that a relationship exists between queen sperm content and effective queen-mating frequency at the individual queen-level, such that multiple mated queens store larger amounts of sperm than do single mated queens. These findings have several interesting implications for the future study of evolutionary aspects of social insect mating systems.

Protective chaos favored by natural selection in metapopulations

Regis Ferriere^{1,2} and Marino Gatto³

The view that group selection should make chaos rare in natural populations has recently been challenged: metapopulations with local chaotic dynamics may persist longer than those with equilibrial or cyclic dynamics. If there are sometimes long-term advantages to chaotic dynamics in local, inter-connected populations, are there ever short-term, individual advantages? We consider whether natural selection, operating on basic life-history traits (including migration rates), may favor parameter values associated with chaos. We use the Henon mapping as a metaphor for local population dynamics involving immigration because (i) the Henon attractor possesses regularity properties that allow us to apply available models of life-history evolution in chaotic populations; (ii) the Henon map represents a "worst case" for the evolution of chaotic life-history phenotypes, due to its propensity to bifurcation reversals across the phenotypic space. We find that assessing the evolutionary optimality of a phenotype amounts to study the dominant Lyapunov exponent of a Schrodinger operator. Conditions for natural selection to promote nonzero migration rates that lead to local chaos, are derived.

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Sex allocation in response to varying host size in the parasitoid, *Achrysocharoides zwoelferi*; a field study.

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Sex allocation theory predicts that where one sex gains more from an increase in size, then that sex should be produced preferentially in favourable conditions. In parasitoids, females generally gain more from increased size. Therefore it is predicted that females should be laid in larger hosts. This has been shown for several species in the laboratory, although not in the field.

In this talk I describe field manipulations in a leaf miner parasitoid which show that females are laid in larger hosts than males. Our results also show that parasitoids use relative host size to determine which sex to lay.

The existence of an Alpine hybrid zone provides further insights into the phylogeography of the meadow grasshopper *Chorthippus parallelus*.

N. Flanagan.

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Evidence for genetic subdivision between geographical races in *C. parallelus* from studies of a Pyrenean hybrid zone and molecular studies of population divergence indicate that the recent evolutionary history of the species has been strongly influenced by the climatic and biotic changes associated with the ice ages.

C. parallelus is now widespread throughout most of Europe, however, for the duration of the last ice age suitable habitat was only available in the southernmost parts of Iberia, Italy and the Balkans, as indicated by the fossil pollen and insect distributions. Post-glacial warming would have led to range expansion northwards with subsequent secondary contact between the previously allopatric populations. This has resulted in the formation of a now well-documented hybrid zone in the Pyrenees between the separate subspecies, *C. parallelus erythropus* in the Iberian peninsula and *C. parallelus parallelus* in the rest of Europe.

Molecular studies have indicated that the Italian population was also distinct from that of Northern European clade, which has similarities to that of the Balkan peninsula. Thus, this study sets out to identify and characterise the hypothesised hybrid zone in the Alps in order to further clarify the proposed scenario of the historical population dynamics of the species.

Reciprocal bulk crosses were conducted between 3 pairs of parapatric populations from either side of the Alps. F1 individuals were examined for hybrid dysgenesis, with male fertility being assessed by the efficacy of spermatogenesis and testis follicle development. The heterogametic males were almost entirely sterile, while measurements of female F1 viability showed no evidence of deleterious effects. Thus, Haldane's rule applies and the role of the X chromosome in hybrid dysgenesis can be invoked to account for this asymmetry. Analysis of backcrosses provides insights into the role played by cytoplasmically inherited factors in this particular example of post-zygotic isolation.

Phenotypically plastic response of egg production to early growth in Atlantic salmon

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Our purpose was to examine the effect of growth rate on egg production in Atlantic salmon (*Salmo salar*), independent of indirect effects through overall fish size. We did this by testing the effect of differences in juvenile (freshwater) and subadult (sea) growth on offspring quality and quantity within and among groups of salmon derived from a common genetic pool. Two groups of Atlantic salmon were created from the same genetic pool of the river Imsa, Norway, one reared naturally and the other artificially from eggs until smoltification (preparation for seaward migration). At smoltification both groups were measured and individually tagged and released to sea together. Individuals of both groups were recaptured when they returned to the River Imsa to spawn. A major difference between these two groups was specific growth rate as juveniles in freshwater, which was 38% higher for hatchery-reared than wild females. This difference did not affect overall allocation to egg production (ovary weight per unit somatic weight) by the two groups, but did affect allocation between egg size and number. Eggs of wild females were 13% heavier, though they produced 23% fewer for a given body size than hatchery females. Specific growth rate in freshwater was also important in explaining variation in egg size within groups, independent of the effects of overall female size. Females thus appear to show a phenotypically plastic response to reductions in resource abundance they experienced as juveniles by increasing egg size which results in a decrease in fecundity. This likely represents a response of salmon to potential growth opportunities for their offspring based on their own early growth experiences.

The Use of Mitochondrial DNA Sequences for Phylogenetic Reconstruction of Higher Order Insect Relationships

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In the work described here, mitochondrial DNA sequences were used to study higher order relationships (subfamilial to ordinal) between orthopteroid insects (Caelifera, Ensifera, Phasmida, Grylloblattodea). Sections of the large & small subunit ribosomal genes & cytochrome oxidase II were sequenced in over 100 species (mostly from Orthoptera *sensu stricto*), yielding a well balanced taxonomic sample. Phylogenies were reconstructed on the separate and combined data sets using various methods. Bootstrap analysis indicated that the rRNA sequence data yielded robust phylogenies at the deepest levels (100-300 mya), but among the more recently diverged Acrididean subfamilies bootstrap values were lower. This latter result might reflect (i) unsuitability of mtrRNA genes for studies among the more recently diverged species, or (ii) a sudden radiation of these taxa during evolution. This first possibility has been investigated in more detail by examining patterns of multiple substitution, and the results of this analysis will be presented. The results will also be discussed in relation to previous hypotheses regarding orthopteran evolution.

Wait or wander: the evolution of mating system in muskoxen

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The distribution of forage resources and females are two important factors influencing the evolution of mating systems in ungulate species. The variation in ungulate mating systems covers males defending (1) entire female home ranges, (2) groups of females, (3) resource patches consistently attracting females, and (4) small territories clustered on mating grounds. In contrast to most ungulates, high Arctic species are exposed to extreme environments and face constraints relating to generally poor forage quality, homogeneous distribution of forage resources and thus female distributions. Consequently, the mating system of Arctic ungulates are expected to deviate from traditionally scenarios.

We present the first results of an extreme field study on evolutionary aspects of the mating system of muskoxen in a natural population in West Greenland. In particular, we present data on (1) distribution of females, (2) male-male competition, (3) mate choice, and (4) age specific mating success. Results are contrasted to data for other ungulates species, concentrating on aspects of sex-ratio, distribution and utilisation of forage, and cost-benefit considerations associated with reproductive performance.

Intraspecific nest parasitism in the barnacle goose: behavioural tactics of parasites and hosts

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Intraspecific nest parasitism in the barnacle goose *Branta leucopsis* was recorded by direct observations of females trying to lay eggs in the nests of other females. This was observed on 36 occasions. Parasitic egg-laying attempts were observed both in mornings and evenings, and lasted on average at least 20 minutes. Parasitic females approached host nests very fast and immediately sat down on or close to the nest. Host females attacked parasitic females intensively, but host males were much less aggressive. Males paired to the parasitic females were sometimes seen, but they never took any active part in the parasitic egg-laying attempts. Parasitic females probably succeeded to lay an egg most of the times, as the clutch size in host nests was on average 0.9 eggs larger than in nests where parasitic egg-laying attempts were not observed. Host females were observed to retrieve eggs laid outside the nest cup. Of 27 known cases, parasitic females made their egg-laying attempts before or at the host's start of incubation on 12 occasions, and after the start of incubation 15 times. It is suggested that parasitic females exploited features in the behaviour of potential hosts, like egg retrieval and low aggressiveness in host males, to succeed in their egg-laying attempts. Nest parasitism seems to be a facultative, 'best-of-a-bad-job' tactic in barnacle geese, as parasitic females were observed to have nests of their own before or after the year they behaved parasitically, but never in that particular year.

OPPOSING FITNESS CONSEQUENCES OF COLOUR PATTERN IN MALE AND FEMALE ADDERS

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Local populations of the adder, *Vipera berus*, are polymorphic for dorsal colour pattern, containing both melanistic (black) and zig-zag patterned individuals. To find an explanation for the maintenance of this polymorphism I examined temporal and spatial variation in morph frequency, and tested for differential selection among morphs using data from a mark-recapture study. Morph frequency did not change through time within a population but varied among populations. Scar frequency was twice as high among melanistic as among zig-zag snakes, and melanistic individuals were easier to capture, indicating that predation may be higher on the melanistic morph. Colour morphs did not differ in growth rate or body size, but analysis of recapture data shows evidence for differential survival among morphs. Zig-zag males survived better than melanistic males, but the relative survival rates of morphs were reversed in females. This difference was consistent through time and may be due to sexual differences in behaviour. Opposing fitness consequences of colour pattern in the two sexes may help maintain colour polymorphism within natural populations of *Vipera berus*.

Predators choosing between patches with standing crop: the influence of learning-rules and input types

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Where prey arriving in a patch is not consumed immediately, it will accumulate. Predators are then confronted with a prey density or standing crop that increases through further input; on the other hand, it will decrease through consumption by predators. In a situation with two patches, three decision rules of predators for choosing a patch are compared. They have a significant influence on the expected predator distribution at equilibrium. For all switching-rules considered here, analytical solutions for the equilibrium are calculated. To test their plausibility for natural situations, I simulated predator distributions on a computer, assuming that each predator gains individual profitability estimates by using a common learning-rule. As long as prey arrives in the patch in constant numbers per time unit, the first rule (where switching depends on the relative difference of the consumption in the two patches) leads to input matching (predator ratio equals prey input ratio) because predators stop switching when consumption in the two patches is equal. The other two rules are probabilistic and will lead to predator distributions where the more profitable patch is underused. The final equilibrium depends on the exact assumptions of the decision rule. All these equilibria also hold if predators suffer from interference. However, if prey input delivered into a patch is a function of the current prey standing crop—e.g. in a reproducing prey population—predator and prey distributions will not reach an equilibrium in most cases: Either standing crops increase indefinitely, or they approach zero. This is true both for situations with and without interference. In a system with competition for standing crop, it is therefore essential to know the type of input and the decision rule used by predators to be able to predict equilibrium predator distributions.

The contribution of new mutations to genotype-environment interaction for fitness in *Drosophila melanogaster*
Fry JD, Lee S & Mackay TFC

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116 . We examined the contribution of new mutations to genotype-environment interaction for fitness in *Drosophila melanogaster*. Twenty lines, each derived from a common, highly inbred base, were maintained at a population size of ten pairs for over 200 generations, in order to allow them to accumulate spontaneous, mildly deleterious mutations. The lines were tested for productivity in five different environments, comprising different food media, temperatures, and levels of competition. The lines showed highly significant genotype-environment interaction for productivity. Estimated cross-environment genotypic correlations for productivity ranged from 0.61 to 0.93, and were usually significantly less than one, indicating that considerable crossing of reaction norms for the fitness measure occurred among the mutant lines. We conclude that spontaneous, mildly deleterious mutations with different effects in different environments could be responsible for maintaining much of the variation leading to crossing of reaction norms for fitness in natural populations.

The selective advantage of phenotypic plasticity
in vertical migration of *Daphnia* in a competition and
predation structured community

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As a case study for plasticity in traits which are constrained by trade-offs, we analyzed the role of phenotypic plasticity for the evolutionary stability of diel vertical migration behavior in *Daphnia*.

We evaluated the competitive ability of *Daphnia* populations that are food limited and that face predation pressure. With non-plastic (fixed) behavior patterns, non-migrating and migrating clones or species can coexist only under quite special conditions. Phenotypically plastic individuals were assumed to adapt rapidly to changing conditions and to be able to always choose an evolutionarily stable migration strategy (e.g. via chemical communication).

We found plasticity to increase a clone's competitive ability but also to enhance the possibilities of coexistence of similar clones with slightly different physiologies.

Therefore, when one includes community structure in an analysis of the adaptive value of phenotypic plasticity, one reveals aspects that are not directly apparent from isolated population models. Hence, selection for plasticity may be more widespread than previously appreciated.

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The present study investigates the effect that different patterns of migration have on the genetic structure of source-sink metapopulations specifically modeling the dynamics of local populations. The model assumes a metapopulation consisting of a single source and s different sink populations and considers the expected number of nucleotide differences between two genes drawn at random from the source-sink metapopulation. I consider three migration models: (a) a constant number of migrants, M , arrives at each sink each generation, (b) the arrival of propagules is synchronized among sinks and their size is a Bernoulli variable taking the values M or 0 with probability u and $(1 - u)$, respectively, and (c) propagules arrive independently at the different sinks and their size is a Poisson variable.

The results show that a collection of interconnected sinks can maintain a substantial fraction of the genetic variability observed in the source population, particularly where migration from the source is continuous over time. The degree of population subdivision might be large, especially if migration from the source is stochastic. Previous demographic models show that ephemeral sinks might have a positive effect on total metapopulation size. These previous results, combined with those of the present study, clearly show that the collection of sinks can significantly increase the total size of the metapopulation and at the same time maintain high levels of heterozygosity. It should also be noted that in a source-sink metapopulation, the effect of extinctions and recolonizations on genetic differentiation is not straightforward. If extinctions are frequent, genetic differentiation is largely precluded, because most of the sink populations are composed of recent migrants from the source. If extinctions are extremely rare, then genetic differentiation is also reduced, due to the increased effect of migration among sinks. Genetic differentiation is maximized when the frequency of extinctions is between these two extremes.

ex chromosome evolution and speciation: the case of the Savi Pine Vole, *Microtus savii* (Rodentia, Arvicolidae)

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rodents are one of the most investigated group to ascertain the relationships between chromosomes and speciation (King 1993). Many types of chromosomes arrangements and their relationships with speciation or at least with lowered fertility in hybrids have been described. The case of the Savi Pine vole can be formative to clarify the role of heterochromatin in speciation. The Savi Pine vole is a small fossorial rodent diffused in Italy and Sicily. The banding of the chromosomes is fairly uniform ($2n = 54$). A few heterochromatic variants however have been described. On the contrary the sex chromosomes are highly variable. In most individuals from the Italian peninsula and Sicily the X chromosome is metacentric with a pericentric C band. The Y chromosome shows minor variations in heterochromatin. A second X is present in Southeast Italy: it has the same length but is acrocentric. These specimens belong to the subspecies *Microtus savii savii* (Krapp and Winking 1976). The subspecies present in Calabria (southwest of the Italian peninsula), *M. savii brachycercus*, show larger sex chromosomes, due to a larger amount of heterochromatin. *Alu-I* and *Da/DAPI* banding suggests a coevolution of at least some parts of heterochromatin between X and Y chromosomes. Hybridization tests performed between specimens of Central Italy and Calabria show an absence of the F_2 which is related to a total breakdown of the male hybrid spermatogenesis. This breakdown could be connected to a failure of the sex vesicle caused by the different quantity and localization of heterochromatin. This example may show how heterochromatin could be related to speciation.

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DEVELOPMENTAL MECHANISMS AND THE INCORPORATION OF EVOLUTIONARY NOVELTIES

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The incorporation of evolutionary novelties into the integrated organism is constrained by many interacting form-function relationships. Organisms must have mechanisms to maintain the match between form and function during evolutionary changes. The most fruitful way to study this problem is to make use of the parallel between developmental and evolutionary changes. Mechanisms that maintain the match between form and function during developmental changes will at the same time facilitate evolutionary changes. One could say that the capacity to cope with developmental changes preadapts organisms for evolutionary changes. The following buffering mechanisms will be discussed:

- 1.) Excess structural capacity
- 2) The decoupling of developmental pathways
- 3) Variable developmental pathways
- 4) Phenotypic plasticity

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Structural innovations are often supposed to play an important role in the development of evolutionary radiations, by triggering a cascade of diverse structural changes. Naturally, changes in the environmental context also play an important role. Changes in the environment and structural changes both modify the interaction between the organism and the environment and thus change selection pressures on potentially all characters. It is therefore fruitful to study structural novelties in a phylogenetic and ecological context.

Structural innovations are often decouplings. Such decouplings release constraints of structural and functional coupling and thereby facilitate increased specialization for a particular function. An example of striking morphological diversity and speciosity associated with a structural decoupling is provided by cichlid fishes (and other labroidei). Liem hypothesized that the versatility of the pharyngeal jaw apparatus is a key factor in the explosive radiation of cichlids into a seemingly endless number of feeding niches. Indeed, on the one hand the versatile pharyngeal jaw apparatus allows cichlids to eat a wide range of prey types so that they can survive in adverse and changing environments, on the other hand the bauplan is versatile in that only small evolutionary changes are necessary to make it suitable for the processing of novel prey items. The shift of insertion of one of the levator muscles was proposed by Liem as the key innovation in the development of the flexible pharyngeal jaw apparatus.

Here a transformation scheme is proposed of the perciform pharyngeal biting mechanism from the generalized condition such as found in the Centrarchidae to the derived labroid condition of the Cichlidae which involves the modification of at least six pharyngeal structures. The transformation scheme is based on mechanical arguments. In this scenario the *key structural innovation* in the development of the functionally versatile cichlid (labroid) pharyngeal jaw apparatus was the decoupling of lower pharyngeal jaws from the upper pharyngeal jaws. This decoupling leads to a cichlid (labroid) type of pharyngeal bite. The initial decoupling facilitated a cascade of changes, each leading to improved biting effectiveness and/or to increased mobility and flexibility of the pharyngeal jaws. The shift of insertion of the m. levator externus 4 which thusfar has been considered the primary innovation in the transformation probably arose secondarily.

Obviously, other mechanisms, e.g. behavioural mechanisms, have played a role in the evolution and speciation of cichlids and other labroids. It is likely, however, that the transformation from the primitive and coupled perciform pharyngeal jaw apparatus to the derived and decoupled one in labroids is the key structural innovation that allowed a remarkable diversification of form and function and that facilitated speciation.

Developmental Instability and Human Functional Brain Asymmetries

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Human brains have a number of typical functional asymmetries. A variety of language functions, for instance, are generally localized in the left hemisphere in most individuals. Many spatial functions are generally localized in the right hemisphere. A number of studies indicate that neural organization at this level is affected by developmental instability. Specifically, developmental instability appears to be associated with atypical functional asymmetry. The most clearly documented case involves handedness. Although human hand preference tends to be bimodally distributed (with about 5-10% of the population preferring their left hand), the relative hand performance underlying these preferences appears to be continuously distributed, with modal performance being moderate right-handedness. Three studies demonstrate that markers of human developmental instability during prenatal development (minor physical anomalies and dermatoglyphic fluctuating asymmetry) is associated with nonmodal relative hand performance -- both left-handedness and extreme right-handedness. Additional work suggests that, although variations in relative hand performance are partly genetic, the heritable variation has more to do with deviation from modal performance (developmental instability) than direction of relative hand performance. More recent evidence indicates that nonmodal cognitive functional asymmetries are similarly associated with developmental instability. Deviations from mean lateralization of both a generally left-lateralized function (language processing, as assessed by a dichotic listening task) and a generally right-lateralized function (processing of emotional facial expression) correlate with fluctuating asymmetry. Preliminary evidence suggests that these atypical patterns of functional organization are furthermore associated with reduced cognitive performance. Implications for an understanding of human functional neural development, evolved functional organization, the phenotypic correlates of human developmental instability, and their evolutionary significance will be discussed.

PHYLOGENETIC PLACEMENT OF THE RECENTLY
DISCOVERED VU QUANG OX BASED ON MULTIPLE GENETIC
LOCI

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Recently, two clearly distinct species of large artiodactyls have been discovered in Vu Quang Viet Nam and adjacent areas in central Laos. Other unique ungulate species are rumored to exist in this same region. The discovery of two or more large mammals in one small geographic area in the late 20th century is remarkable. Even more exciting is the fact that preliminary genetic and morphological analyses suggested that these new species may be relatively primitive taxa that have no close living relatives.

In this report, we analyze the evolutionary affinities of the Vu Quang ox (*Pseudoryx nghetinhensis*) which has variously been placed as a relative of Bovini (buffalos+cattle), Caprinae (goats, sheep, and relatives), or "antelopes." Analyses of multiple genetic loci from the nuclear and mitochondrial genomes clearly discount the close relationship of *Pseudoryx* and the caprines that is suggested by skeletal characters. Instead, the Vu Quang ox appears to be derived from within the Bovinae, a group that includes cattle, buffalos, and some "antelopes." The combined analysis that is based on over four kilobases of comparative sequence information implies that *Pseudoryx* is a phylogenetic relict that has no close extant relatives.

A comparison of private alleles, G_{ST} and θ for quantitative estimates of gene flow levels: *Androniscus dentiger* as a study case.

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Theory of population genetics provides more than one method for estimating gene flow levels among natural populations, using genetic data. Direct and indirect methods are available: the former aim to estimate gene flow due to dispersal of individuals, the latter are based on the spatial distribution of descriptors of gene pool.

Direct measurements are constrained by time and space scaling: results obtained in such a way may be affected by the restricted time during which observations were made, providing a momentary picture. Furthermore difficulties arise in detecting long distance movement of individuals. On the other side indirect methods, even though requiring some restrictive assumptions, give results better interpretable as average level of gene flow, reflecting on the whole evolutionary processes and historical factors underlying genetic variation observed. Concerning cave organisms and more generally animals characterized by a limited dispersal ability, indirect methods appear to be preferable particularly when the geographical scale considered is large.

Under these circumstances it was studied a woodlouse, *Androniscus dentiger* (Isopoda, Oniscidea, Trichoniscidae), inhabiting humid edaphic environments and both natural and artificial caves. Allozyme data on a set of 19 loci were used to estimate levels of gene flow among populations. Quantitative estimates of Nm were obtained by different methods. Private alleles (Slatkin and Barton, 1989), G_{ST} (Nei, 1977) and θ (Weir and Cockerham, 1984) were used, after testing that restrictive conditions of population genetic model and neutrality of alleles have been met. The possible occurrence of isolation by distance was investigated by means of spatial autocorrelation analysis. Slatkin (1993) showed that isolation by distance can be well described by a logarithmic relationship between gene flow levels and geographic distance. We tried to verify this issue for *Androniscus dentiger*. Results show that different approaches well agree in providing similar Nm estimates. G_{ST} and θ are closely related as expected when treating with low migration species. Private alleles methods provides slight underestimated Nms in respect of those obtained from F_{ST} estimators. This may depend on the high degree of population structuring. In general no ongoing gene flow can be assumed among *A. dentiger* populations, even though geographically related. Nevertheless some pattern of gene flow occurred in the past can be still detected. Biological significance of results obtained are discussed.

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EFFICIENCY OF DETECTING MULTIPLE INSEMINATIONS IN ANTS
AT DIFFERENT LEVELS OF SPERM BIAS
USING MICROSATELLITE MARKERS
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Polyandry in eusocial Hymenoptera poses an interesting evolutionary problem by its effect of reducing the high intracolony relatedness, which is considered central for the origin and maintenance of eusociality. The major hypotheses proposed for explaining polyandry in eusocial insects are sperm limitation, benefits of genotypic diversity among offspring, and the effect of polyandry on optimal sex allocation patterns. Data on polyandry in Hymenoptera are still rather scarce. In ants, it has mostly been measured from allozyme genotypes of workers from laboratory rearings. A quicker method, now available, is to assign the minimum number of inseminations by amplifying DNA-microsatellites directly from the sperm contents of spermathecae. The high variability of microsatellites gives a high probability of detecting all inseminations. Moreover, spermatheca-PCR overcomes the risk of misdetecting polyandry because of uneven sperm use from different males, which is a serious risk when number of matings is assessed from the genotypes of the offspring.

Sperm bias seems to be the rule at least in ants, the contribution of the majority male ranging from 67% to more than 90%. This means, that in the spermatheca-PCR, DNA from different males would be unequally represented. Since PCR is an exponential process, the minority males might remain undetected. In order to assess the detection efficiency of spermatheca-PCR, *Atta colombica* -males of known genotypes were dissected, sperm solutions were prepared and their concentrations determined by sperm counting. Artificial sperm mixes were then made in varying ratios, to simulate different sperm bias situations in the spermathecae of multiply mated queens. These mixes were used as template in PCR at very low stringency. The results so far imply that, with increasing sperm bias, the amplification from the minority males weakens, until at an extreme sperm bias (1:9) they cannot be detected at all. The detection efficiency also seems to depend on the particular alleles males carry, since shorter alleles are often preferentially amplified in the PCR-reaction. These preliminary results suggest, that assessing the number of inseminations by means of microsatellite PCR from spermatheca should be used with caution, particularly if significant sperm bias is known to occur. More species from the ant genera *Atta*, *Camponotus* and *Formica* are currently being investigated.

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FROM POPULATION BIRTH TO EXTINCTION: SMALL SCALE METAPOPULATION DYNAMICS IN *SILENE DIOICA*.

In Skeppsvik Archipelago in the Gulf of Bothnia, northern Sweden, land uplift continually creates new islands which are eventually colonised by plants. As a result, islands and their plant populations differ in age. As these islands go through a series of successional replacements, populations of plant species occurring in early succession go extinct. An archipelago-wide study of the early successional, dioecious, perennial herb, *Silene dioica*, revealed that the genetic variance of newly founded populations was significantly higher than that of older populations, thus confirming the predictions of the Whitlock-McCauley age-structured metapopulation model. Decaying populations on their way to extinction were also more differentiated. This study, however, indicated significant structuring within island populations, and field observations suggested that age differences in older and younger parts of an island could increase differentiation among patches in a manner similar to that observed at the between island level. To investigate these ideas, detailed studies were carried out within four islands. We show that the size breeding units within *S. dioica*, populations maybe less than 2m^2 . By grouping patches into age-classes, we also show that levels of differentiation in newly colonised and decaying patches are higher than in actively growing patches of intermediate age which suggests that age-structured metapopulation dynamics occur over small spatial scales within single islands. Whether or not an island is exposed to excessive wind and wave action or is protected is shown to affect patterns of differentiation within islands, in particularly, isolation by distance is observed within populations on protected islands whereas it does not occur on exposed islands.

An examination of genetic diversity within and between provenances of *Cedrela odorata* (mahogany) using RAPD markers.

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The mahogany family (Meliaceae) includes a number of economically important tropical timber species, such as *Swietenia macrophylla* King (American mahogany) and *Cedrela odorata* Linn. (Spanish Cedar), and accounts for a significant proportion of world trade in this commodity. Two of the three neotropical mahogany species are now considered endangered because of over logging and are listed on Appendix II of the Convention on International Trade in Endangered species (CITES). Much of the mahogany that remains exists as small fragmented populations on farms. The viability of such small, isolated populations depends, therefore, on adequate gene flow occurring between them, to counter the processes of genetic erosion.

Despite their commercial value, very little is known about the extent of genetic variation within these species. Current research is therefore aimed at the application of molecular techniques, principally RAPDs (Randomly Amplified Polymorphic DNAs), to assessment of the degree of genetic variation within and between provenances of *Cedrela odorata* and, furthermore, to examining the effect of selective logging on genetic variation.

Fifteen random primers have been used to generate RAPD banding patterns in individuals from provenances of *Cedrela odorata* occurring throughout Costa Rica. No RAPDs have been identified as unique to a particular provenance. However, UPGMA analysis indicates that all provenances collected from north of the mountain range that runs across the centre of Costa Rica have banding patterns that are distinct from those of provenances south of these mountains. This correlation between the geographic origin of a provenance and its RAPD phenotype is of considerable interest, since it is thought that the mountain range marks the boundary between the North and South American landmasses that were separated from each other until the formation of a landbridge 5.7 million years ago. Therefore, these distinctive RAPD phenotypes may lead to new insights into the evolution of the genus.

Shannon's Diversity Measure has been used to quantify genetic diversity and partition it into between- and within- provenance components. Results indicate that 60% of variation exists between provenances.

A molecular phylogeny of the *Drosophila willistoni* sibling species based on *period*, *Adh*, and *Cytochrome oxidase subunit I* DNA sequence:

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The *Drosophila willistoni* sibling species are a group of six Neotropical species (subgenus *Sophophora*). The species (*D. willistoni*, *D. insularis*, *D. tropicalis*, *D. paulistorum*, *D. pavlovskiana* and *D. equinoxialis*) are essentially morphologically indistinguishable but exhibit complete reproductive isolation. Because of different degrees of premating isolation, the existence of polytypic species, and the fact that *D. paulistorum* is a complex of 6 semispecies, the *D. willistoni* sibling species are an ideal group for the study of speciation. Studies of the genetic variation within the group have primarily focused on allozyme polymorphisms and chromosomal inversions, and there is very little DNA sequence data as yet. The phylogeny of the group has not yet been completely resolved, making speciation studies difficult.

Different data sets have produced various conflicting hypotheses of the evolution of the group. Using *D. nebulosa* as the nearest outgroup, all data sets agree that *D. insularis* is the most basal of the taxa. The arrangement of the other species is disputed (although *D. pavlovskiana* is the sister taxon of *D. paulistorum* since it was originally described as a *D. paulistorum* semispecies). Allozymes place *D. tropicalis* and *D. willistoni* in one clade that is the sister clade of *D. paulistorum* (and *D. pavlovskiana*) and *D. equinoxialis*. DNA-DNA hybridization data indicated that *D. willistoni* and *D. paulistorum* form one clade that is a sister clade to *D. equinoxialis* and *D. tropicalis*.

Presented here is a new data set consisting of two nuclear genes including approximately 1.2 kb of the *period* (*per*) locus, and 1.2 kb of *Alcohol dehydrogenase* (*Adh*), as well as 495 bases of mitochondrial *Cytochrome oxidase subunit I* (*COI*). Again, all data sets agree that *D. insularis* is the most basal taxon. *COI* alone cannot resolve the species as they are so closely related. *Adh* similarly yields different topologies for different methods of tree building. The *period* data, both alone and in combination with the other data sets supports a topology in which *D. equinoxialis* and *D. paulistorum* form a clade with *D. willistoni* as the next species, followed by *D. tropicalis* and finally *D. insularis*.

The population-dynamic behaviour exhibited by one or a group of interacting species is determined by the demographic and life history parameters of the animals or plants involved. These parameters are moulded by natural selection, but the process of evolution itself may be influenced by population dynamics. The interplay between population and evolutionary dynamics will be explored using models of the interaction between insects and their natural enemies, particularly parasitoids and pathogens. For example, age-structured models of insect-natural enemy interactions often predict cycles with a period of one host generation if the generation time of the natural enemy is about half that of the host. There are good field data supporting this prediction. In an interaction with this type of dynamics, selection acting on the generation time of the host is strongly stabilizing, while that on the generation time of the natural enemy is strongly divergent. The outcome of the joint population and evolutionary dynamic process depends on the speed with which each party responds to selection, and on the strategy set available to each. We shall also explore insect host-pathogen dynamics and, if worked planned for the next couple of months goes well, host-parasitoid evolution in a metapopulation.

A contact zone of three species of Crested Newts *T17*
(*Triturus cristatus* superspecies, Salamandridae)

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The ranges of three species of Crested Newts, *Triturus cristatus*, *T. carnifex* and *T. dobrogicus*, meet in Lower Austria. To study distribution and potential hybridization of these species, we analysed morphometric and allozymic variation in eight populations from the Waldviertel region and in several allopatric reference samples. For the sake of conservation, no newts were removed from their habitats and only homogenates of tail-tips (which are readily regenerated) were used for the electrophoretic investigations. Hence, genetic data are limited to four loci with species-diagnostic alleles.

In an area where contact between *T. cristatus* and *T. dobrogicus* could be expected from previous distribution maps, populations of *T. carnifex* occur north of its formerly recognized range and thus separate the ranges of the two other species. However, allozyme markers derived from all three species were detected in most of these populations. Genotype distributions conformed to Hardy-Weinberg expectations in most cases. Morphometric results allowed clear separation of *T. dobrogicus*, but not of *T. cristatus* and *T. carnifex*.

The position of the hybrid zone in the *Triturus cristatus* superspecies is compared with the contact zone between the Fire-bellied Toads *Bombina bombina* and *Bombina variegata* which occur in the same breeding habitats.

Let us assume that diploidy saves multicellular individuals with large body mass and large genom value from somatic mutations^[1]. The heterozygotic part of genome is effectively haploid and should be small. Let us denote the random autosomal heterozygosity of homogametic sex as H_a , and effective heterozygosity of (containing with) nonparing sex chromosomes of heterogametic sex by H_0 . So the total heterozygosity of heterogametic sex equals $H = H_a + H_0$. We assume that in normal condition the inequality is fulfilled:

$$H_a + H_0 \leq H_c. \quad (1)$$

Here the normal individual with $H \leq H_c$ have the maximal fitness and competitive capacity. When external condition is distorted the individuals with deleterious substitutions having heterozygosity up to the letal threshold, H_L : $H_c < H < H_L$. can accumulate in the population. The hybrid of two species have additional hybrid heterozygosity H_h . The total heterozygosity of the hybrid equals $H = H_h + H_a$ for homogametic sex and $H = H_h + H_0 + H_a$ for heterogametic sex. For mammals $H_a = 0.07$, and $H_0 = 0.05$, and hence $H_c = 0.12$ ^[2,3]. Hybrid zones are small in natural condition and we can assume that hybrids are absent. It means that the following condition is true:

$$H = H_h + H_a > H_c. \quad (2)$$

The Haldane's rule^[2] is that in artificial conditions only hybrids of heterogametic sex are absent or nonfertile. This statement is equivalent to the condition:

$$H = H_h + H_a + H_0 > H_L > H_h + H_a. \quad (3)$$

We have from equations (1) and (2): $H_h > H_0 = 0.05$. Assuming $H_h \approx H_a = 0.07$ we have from (3): $0.17 > H_L > 0.12$ for mammals in average. For mammals with a very small random autosomal heterozygosity $H_a \ll H_0$ living in extremal external conditions (like cheetah and polar bear)^[2] we have: $H_h, H_L < H_0 + H_a$ i.e. $0.07 < H_L < 0.12$.

Thus the small size of hybrid zone in natural condition and Haldane's rule in artificial conditions can be explained by existence of two thresholds of heterozygosity: H_c (the limit of sensitivity of competitive interaction of individual inside natural population) and H_L (lethal threshold of heterozygosity) for species of large genome and body mass. $H_L = 1$ for the species having small genome value and small body mass that capable live in haploid phase (like fungi, mosses and insects) and

PHENOTYPIC PLASTICITY IN APHIDS IN RESPONSE TO HOST PLANTS AND SECONDARY CHEMICALS

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The evolutionary importance of phenotypic plasticity in parasite speciation has been largely neglected. In this experiment *Aphis fabae* clones were reared on black bean (*Vicia faba*) and nasturtium (*Tropaeolum majus*), and fitness indices were measured. The host plants caused significant differences in life history traits, morphological characters and fluctuating asymmetry.

In a parallel experiment, artificial diets were used in order to determine aphid's phenotypic response to specific secondary chemicals. Ten clones of *Myzus persicae* were reared on (i) toxin-free and (ii) diets with specific plant secondary chemicals and fitness and morphological traits measured.

We discuss the implication of our results in the context of "phenotypic" host race formation and the consequences for speciation.

The intergenic spacers of the 5S rDNA genes. A suitable marker for phylogenetic analyses?

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The 5S rDNA genes are tandemly arranged in the genome of *Drosophila*. The 5S rDNA repeats of nine species of the *Drosophila obscura*-group were specifically amplified by PCR and characterized in order to analyze the evolution of this tandemly repeated DNA.

For the coding regions of the 5S rDNA genes no differences were detected between the species, only few clone-specific nucleotide exchanges were observed. The non-coding intergenic spacers of the closely related sibling species *D. subobscura*, *D. madeirensis* and *D. guanche* are almost identical, however, they differ substantially between the other more distantly related species. A sequence alignment reveals that - beside some single nucleotide exchanges - the homogenization of short insertions/deletions is the main source for the interspecific sequence variability. As a consequence, it is almost impossible to align the intergenic 5S rDNA spacers from distantly related species, e.g. from the American species *D. pseudoobscura* and from any European species of the *D. obscura*-group.

The phylogenetic networks based on the 5S rDNA spacer sequences were compared to those derived from other data. It can be concluded that the use of 5S rDNA spacers as a phylogenetic marker is rather limited; there are too few informative differences between closely related species and already too many between more distantly related ones.

Polymorphic sex chromosome mechanism in two species of *Cacopsylla*
(Homoptera, Psylla)

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The karyotype of *Cacopsylla sorbi* and *C. mali* (Homoptera, Psyllidae) from six populations has been investigated. The males of these species were found to be dimorphic with respect to their sex chromosome constitution and the autosome number. Three types of sex chromosome constitution have been found: Type A (XO) had been described for *C. sorbi* ($2n=24+XO$) (Soumalainen, Halkka, 1963); Type B (XY) - in *C. mali* ($2n=22+XY$) (Maryanska-Nadachowska et al., 1992, here) and Type C (X_1X_2Y) - in both species - *C. mali* ($2n=20+X_1X_2Y$) and *C. sorbi* ($2n=18+X_1X_2Y$). A reduction of the chromosome number in Type B and Type C has been obtained. The behaviour of the sex chromosomes during meiosis has been studied. Some abnormal complements have been observed at MI in *C. sorbi*, Type C, as a result of inverted division of the X-chromosomes.

In the present investigation a scheme has been proposed indicating how the XO type, through X-chromosome fusion gave rise to neo X_1X_2Y type. The genus *Cacopsylla* belongs to the most advanced subfamily of Psyllidae - Psyllinae and the chromosome polymorphism in this group is a confirmation of the opinion that number of aberrations is higher in the advanced and specialized forms (Kiauta, 1969; Kirillova, 1988), and if they did not possess their flexibility, they would be unable to adapt themselves to changing conditions.

TRANSMISSION DYNAMICS OF MALARIA PARASITES

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In order to survive, parasites need to optimise their division of resources between within-host replication and between-host transmission. The local conditions that parasites encounter will affect the optimal solution, and therefore transmission strategy should be altered by environmental factors such as superinfection.

Mixed-genotype infections of malaria are common in the field, and in experimental mixed infections of *Plasmodium chabaudi* in mice, clonal replication within the host can be suppressed by the presence of another clone by up to 90%. When within-host replication is inhibited in this way, natural selection should favour genotypes which increase transmission-stage production.

To test this prediction, we inoculated two *P. chabaudi* clones into mice and followed their within-host replication and their transmission success in mosquitoes, using monoclonal antibody and PCR analysis. Mixed-genotype infections were significantly more infectious to mosquitoes than control single-clone infections. Furthermore the minority clone in mice can become numerically dominant in mosquitoes. This is consistent with a facultative up-regulation of transmission stage production in the presence of superior competitors.

Thus, the transmission rates of a parasite clone can be altered in mixed-genotype infections and, contrary to some epidemiological models, numerical dominance in a host infection may be a poor predictor of transmission probability.

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ISOLATION BY DISTANCE IS RECOGNIZED IN AN ITALIAN PROVINCE
THROUGH SURNAMES AND HLA GENES

--P16

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Italian provinces may constitute a basic geographic unit that is big enough to be genetically structured and, at the same time, sufficiently small to be intensively analyzed. Surnames are widely accepted as selectively neutral genetic markers and as such used to study random genetic drift and migration. Sampling surnames from the telephone directory may constitute a relatively simple way to obtain information about the genetic structure and the demographic peculiarities of a geographic region. We proved the efficiency of sampling surnames from the telephone directory to cast light on the genetic and demographic pattern of the province and to prove the sampling efficiency. The 189 communes of the province of Pavia were grouped into subregions composed of geographically clustered communes and the relationships among them were examined using principal component analysis (PCA) and cluster analysis.

Furthermore the combined use of surnames, which simulate selectively neutral genetic markers and HLA genes, which are extremely polymorphic and at the same time peculiar genetic markers because of their involvement in the immune response, may constitute a useful tool for the genetic survey of a small area.

We found an almost perfect coincidence between HLA genetic structure and surname pattern, in the province of Pavia. Both type of data indicate that the two main local rivers, which cut the area into three subregions, represent genetic barriers. Our results go beyond the boundaries of a mere population genetics speculation, as they can be very useful in local epidemiological surveillance.

Variation in Mating Rate in Hermaphrodites Maintained by a Sexually Transmitted Disease

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A hybrid model for the evolution of promiscuity in a haploid, hermaphroditic population with non-overlapping generations, in which each generation suffers an epidemic of a sexually transmitted disease, is examined. The dynamics of the disease are described using a differential-equation model working within generations, while the evolutionary genetic dynamics are modelled using a discrete-time approach with non-overlapping generations. The results, mostly obtained using numerical methods, show that a sexually transmitted disease can maintain differences in mating rate within a population of hermaphroditic individuals.

Differences in mating rate translate into differences in reproductive success through male function but also into differences in reproductive fitness through female function due to differences in exposure to contagion. Large differences in mating rate may lead to protected polymorphisms while smaller differences in mating rate lead to fixation of the allele leading to higher or lower mating rates depending on the impact of the disease. Diseases with a high impact generally favor lower mating rates. The mechanisms discussed here are different from the ones in the Hamilton-Zuk hypothesis since the infection status of an individual does not affect its mating success, neither directly nor indirectly. However, the results do not carry over to dioecious organisms. Dioecy is one of several possible strategies, that an organism could exploit in order to evade the cost due to sexually transmitted disease.

PHENOTYPIC AND GENETIC APPROACHES TO EVOLUTION: A NEW SYNTHESIS?
137a.

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Phenotypic approaches to evolution are commonly used in theoretical studies of animal behaviour. However, a look at n-locus population genetics theory shows that the effects of recombination may severely disturb the phenotypic picture of evolution. This leads to the following puzzle: why can phenotypic analysis of behaviour be so successful if it is not safely based on genetic grounds? A new line of reasoning helps to answer this question and leads to the 'streetcar theory of evolution'. Using the streetcar paradigm it can be demonstrated that phenotypic fitness maxima and evolutionarily stable strategies have a solid foundation in population genetics theory. In this sense the new theory extends the evolutionary synthesis that took place during the first half of this century.

Molecular markers and the study of evolution and systematics in tropical tree legumes.

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Molecular markers, whether protein or DNA-based, have become increasingly important in the study of evolution and systematics in plants and the relative values of such markers for the analysis of particular questions are starting to become apparent. Isozyme analyses have proven very valuable for the study of genetic diversity and population structure. An analysis of 30 populations (approximately 900 families), from throughout the African range, of *Acacia albida* (Del.) A. Chev. showed the occurrence of three major regions of genetic diversity: West Africa; Ethiopia/Sudan; East/South Africa. At the DNA level, restriction fragment length polymorphism (RFLP) analyses have been valuable for the study of phylogeny and systematics, whilst randomly amplified polymorphic DNA (RAPD) analyses have been useful for the study of genetic diversity and hybrid identification. Chloroplast DNA RFLP analysis of *Leucaena* Benth. has provided valuable insights into the evolution of the genus, whilst RAPD analysis has enabled the genetic diversity of a number of species to be described. Particularly valuable in *Leucaena* has been a combined approach of RFLP and RAPD analyses for the identification and characterisation of naturally occurring hybrids.

Evolutionary interactions between cytoplasmic sex ratio distorters, host fitness and sex ratio.

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Uniparentally inherited factors are selected to bias host sex ratio towards the transmitting sex, or increase the fitness (survival or fecundity) of infected hosts. Maternally inherited parasitic factors may achieve these criteria by a variety of means, including direct distortion of primary sex ratio towards females and sex determination distortion. Under certain conditions, compensatory (male-biased) sex ratios are selected for in uninfected hosts. We demonstrate that the point of expression of host sex ratio (maternal versus offspring control) does not affect the evolutionary stable host sex ratio in infected populations.

We examine the consequences of infection by parasitic sex ratio distorters on host fitness, with particular regard to distorters of sex determination. A microsporidian parasite of the amphipod *Gammarus duebeni* operates by these means; converting putative males into phenotypic females. The parasite may be able to manipulate host gender in this instance as *G. duebeni* exhibits environmental sex determination (ESD). We demonstrate that sex ratio distorters that override ESD may have a negative impact on host fitness as they impose suboptimal gender with respect to fitness-related environmental variables.

Fertility of house mice from a chromosomal hybrid zone in the Italian Alps.

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Carriers of heterozygous Robertsonian (Rb) fusions are expected to have a lower fertility than homozygotes, since heterozygous fusions may cause malsegregation at meiosis. An accurate estimate of the fertility of Rb heterozygotes is important to the understanding of the formation of chromosomal races, the dynamics of chromosomal hybrid zones, and whether Rb fusions cause speciation. The house mouse is an especially versatile model with which to study these questions since more than 60 chromosomal races and ten chromosomal hybrid zones have been documented for this species. For the present study, mice of three races from a chromosomal hybrid zone in Upper Valtellina, Italy, were used to produce three types of highly-heterozygous hybrid. Hybrids heterozygous for various fusions were also caught in the field. Five measurements of fertility were made for each individual. Despite comparatively high rates of nondisjunction and germ cell death, the litter sizes of heterozygous males and females were similar to those of homozygous Rb mice. We discuss how relative fitness of mice with different karyotypes may affect gene flow and speciation between races in Upper Valtellina. This intensive study is unusual in that fertility estimates were calculated for many female and wild-caught heterozygotes.

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Hybridisation ability between populations of weedy *Brassica campestris* and varieties of oilseed rape (*B. napus*): fitness of parental, hybrid and back-cross plants.

An important aspect of risk-evaluation of a transgenic crop is to study its possible hybridisation with related species. Cultivated *Brassica napus* is known to hybridise relatively easily with cultivated and weedy *B. campestris*, whereas back-crossing of the hybrids to either parental species is more difficult, but possible. Back-cross plants have been identified in field experiments and in weedy populations of *B. campestris*¹, suggesting that genes from *B. napus* may introgress to weedy populations of *B. campestris*. In an ongoing project we study dynamical aspects of the hybridisation between *B. campestris* and *B. napus*, with emphasis on genetic variation for hybridisation ability and effects of competition between pollen and seeds of the two species.

Individuals, varieties and populations of *B. napus* and *B. campestris* may differ in their inter-specific cross-compatibility, and a possible selection against the hybridisation may take place at different life stages of the plants. Two crossing generations are analysed to characterise the F₁ and the backcross/F₂ generation. In the first generation, three weedy Danish *B. campestris* populations and three varieties of *B. napus* have been crossed in all possible combinations, including intra-populational crossings. After harvesting, the fruit and seed set has been estimated, and the seeds transferred to the field. The resulting plants will be monitored for important fitness components during their life cycle. By comparing the performance of hybrids and non-hybrids from different combinations of populations and varieties, genetic variation for hybridisation ability among individuals and populations/varieties will be estimated.

In nature, stigmas of *B. campestris* and *B. napus* often will receive a mixture of pollen from both species. Competition between pollen and seeds of different parentage within a pod could potentially increase fitness differences compared to pods with a single species as donor. To study this, we have applied different mixtures of *B. napus* and *B. campestris* pollen to stigmas of both species. By comparing the applied proportions to the proportion parentage found in the seeds (determined by isozymes), it may be possible to detect selection against hybrids or non-hybrids.

¹Jørgensen, R. B. et al. 1995. Acta Horticulturae (in press).

Effective population size of a metapopulation - Phil Hedrick, Arizona State University, Tempe, AZ, USA. Population structure has long been recognized as a major influence on the maintenance and loss of genetic variation although it has generally been assumed that subpopulation sizes remained constant over time, i.e., either subpopulations do not go extinct or if they do, they are immediately recolonized. It has been shown in recent years that if a population exhibits metapopulation dynamics, i.e., patches in which subpopulations exist become unoccupied because of local extinction and they are not immediately recolonized, that many of the generalizations of earlier studies of population structure may not hold. In particular, the effective size of a metapopulation may be much less than the census number. The process through which metapopulation dynamics reduces genetic variation has been termed the coalescence of the metapopulation, i.e., the loss of genetic variation being traced back to a few individuals that are the ancestors of all the individuals in the present metapopulation. I have estimated the effective size of a metapopulation and its subpopulations by determining the loss of heterozygosity per generation. There are a number of parameters that can influence the effective population size of a metapopulation, and I have endeavored to systematically explore their influence. For example in a given model, the carrying capacity of a subpopulation may have only a small influence on the effective size so that the effective size of a metapopulation may be very much less than the census number. Rapid turnover, extinction and recolonization, also greatly reduces the effective metapopulation size. Gene flow, at times other than recolonization can actually increase the effective size of a metapopulation, a finding counterintuitive to that from traditional population structure models which have shown that more genetic variation could be retained with lower levels of gene flow. Although the commonness of dynamics like that in a theoretical metapopulation in natural populations is not clear there do appear to particular instances in which habitats are fragmented that metapopulation dynamics may be an appropriate description of the population structure at a regional level. There has been increasing interest in the impact of metapopulation structure on genetic variation in endangered species and I will discuss, as an example, the potential impact of metapopulation dynamics on the genetic variation observed in cheetahs.

Seed structure and group delimitation in *Solanum* sect. *Pteroidea* Dunal.

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Solanum section *Pteroidea* is a small group of tropical understorey herbs. The species of section *Pteroidea* are scarce in the habitats in which they occur and are rarely collected. The group as presently delimited is defined by possession of strictly axillary inflorescences, but there appear to be two very distinct groups based on flower size and morphology within the section. In addition to this, species in the section have either pinnately compound or simple leaves. This complex pattern of variation has resulted in taxa being placed in widely separated parts of the genus by a succession of authors. New characters are clearly needed to help resolve relationships in the group.

The structure of seeds has been useful for resolving the relationships among species where morphological characters exhibit complex patterns of variation. In Solanaceae, lateral cell wall structure can be seen after enzymatic digestion of the outer testa wall. Gross seed morphology has been used successfully to distinguish taxa in Solanaceae, but the characters have not been formally analysed.

As part of a monographic study of *Solanum* sect *Pteroidea* the above technique was used in order to determine whether seed characters could identify groupings within the section, and whether these are congruent with other morphological variation. Preliminary work suggests that *S. anceps* Ruiz & Pavon has a seed wall structure that is unlike other solanums.

Sperm competition in the yellow dung fly Scathophaga stercoraria: adding the female perspective.

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Sperm competition has traditionally been modelled exclusively from the male perspective; females have been taken as passive during the entire process. However, female dung flies, like other Diptera, have a complex reproductive system with three separate spermathecae and can to some extent store the sperm of different males separately.

model the effect of multiple storage organs on the outcome of sperm competition as measured by the fertilisation success of second-mating males, the P_2 value. There is an effect of the size of the female's storage capacity: P_2 values are higher when mean ejaculate size is larger than the total storage capacity. Under otherwise similar conditions, P_2 values are higher with two storage organs than with one, probably because the second male can better displace previously-stored sperm. Females benefit from separating the ejaculates of different males because they can then better influence the paternity of their offspring, especially in instances of conflict between sexes. This benefit increases non-linearly with greater degree of female control over the fates of ejaculates. As females of many animal groups may be able to spatially separate the sperm of different males, these results could have wide general significance.

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We develop a simulation model for analysing gene flow in geographically structured populations based on information about local population sizes and dispersal patterns. The model is used to predict genetic differentiation between natural populations of Atlantic salmon for which there is data on the number of reproducing individuals and dispersal patterns. Predictions from the model are then tested against estimates of genetic differentiation based on an enzyme electrophoretic analysis of the study populations. Analyses suggest that the amount of genetic differentiation (Wright's F_{ST}) predicted from the simulation model is significantly lower than that determined by the electrophoretic analysis. Reasons for this discrepancy may include differences between actual and effective population sizes, and reduced fitness of dispersing relative to philopatric individuals.

EVOLUTIONARY BIOLOGY OF FUNGI: PROMISES AND PROBLEMS

Rolf F. Hoekstra, Wageningen

Compared to animals and plants, fungi have been largely neglected by evolutionary biologists. Recent years however witness a growing interest in population and evolutionary biology of fungi. This talk will concentrate on ascomycetous fungi and will review experimental and theoretical work on evolutionary problems for which fungi seem especially attractive as study objects. Research on ascomycetes shares a number of advantages with that on other micro-organisms: easy and cheap to cultivate in the lab, short generation time, and for a number of model species (yeast, *Neurospora*, *Aspergillus*) excellent genetics. A weak point so far is an often considerable lack of information on the ecology of natural populations. Problem areas in which fungi offer very good opportunities for evolutionary research include between species interactions (mutualism and parasitism), evolutionary dynamics of parasitic DNA and somatic interactions between individuals. The latter subject bears on questions regarding the evolution of individual genetic integrity and here the potential of fungi to sometimes form somatic connections (anastomosis) with conspecifics can be exploited in experimental evolutionary research.

Genetic structure of the wood decay fungus *Fomitopsis rosea* in Sweden and Russia.

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The coniferous forests of Sweden are intensely managed and the late successional species are often found in small and fragmented populations. Small populations are prone to loss of genetic diversity by processes such as genetic drift and inbreeding. The impoverishment seen in this area has its major causes in the intensive management of forest and agricultural lands.

We focus on the possible reflection of landscape ecological structures in the genetic structures of the populations in these landscapes. We have a particular interest in how fragmentation of a species distribution will affect the population genetics. Two wood decay fungi are studied; The common wood decay fungus *Fomitopsis pinicola* in a comparison with the more restricted *Fomitopsis rosea*.

Fomitopsis rosea is an outcrossing fungus with a bipolar mating system. Studies with Arbitrary primed PCR show that *Fomitopsis rosea* has very little genetic variation in Sweden where this fungus is rare. Data will also be presented about the genetic variation in the Komi area on the Russian taiga and also the genetic differentiation between Swedish and Russian isolates of the fungus.

We currently develop sequence based DNA-markers for population studies. These markers are derived with Arbitrary Primed PCR DNA as an intermediate step and further characterised by sequencing. We will show how these markers can extend the understanding of population processes from current gene flow to historical data such as genetic bottlenecks in the past and historical migration.

Homeobox genes and chordate evolution

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Homeobox genes are giving new insights into the co-evolution of molecules and morphology. We are comparing the organisation and expression of homeobox genes, and other genes with important developmental roles, between vertebrates and protochordates. The *Hox* gene family (a subgroup of homeobox genes) expanded by tandem gene duplication to form a large gene cluster before chordate origins. This ancestral gene cluster duplicated close to vertebrate origins, creating a much larger suite of these regulatory genes, alongside elaboration of the body plan. In contrast, amphioxus retains a *Hox* gene cluster similar to that inferred for vertebrate ancestors: a molecular correlate of its archetypal body organisation. Examination of other genes reveals that this is not an isolated correlation. We find that duplication of genes was very widespread during vertebrate evolution, whilst the lineage leading to amphioxus experienced greater (but not absolute) genetic stasis. Comparisons of gene expression patterns between amphioxus and vertebrates reveal that new vertebrate genes were co-opted for new accessory roles; we argue that extensive gene duplication, plus genetic co-option, was necessary for origin of the complex vertebrate body plan. The mutational mechanism by which these gene duplications occurred is of great interest; data addressing this question, and the implications for human genome organisation, will also be discussed.

Until recently, worldwide *Drosophila melanogaster* was considered a single panmictic population (Henderson & Lambert, 1982; Kreitman 1983; Kreitman & Aguade, 1986). It is now known that considerable population subdivision exists for this species in Africa (Begun & Aquadro, 1993; Begun & Aquadro, 1994). Congruent with the molecular divergence, it has been shown that Zimbabwe populations are sexually isolated from other worldwide strains in that Zimbabwe females refuse to mate with males from the other strains (Wu, et al., 1995). No postmating isolation exists between these populations, indicating sexual isolation has evolved recently. Preliminary genetic results reveal that although male courtship and female preference must evolve in concert, these traits represent unlinked genetic systems in this population. The X chromosome plays no role in determining either trait. The genetic architecture of premating reproductive isolation in this system appears to be autosomal, polygenic and strictly additive which contrasts directly to the genetic pattern of premating isolation seen between well-differentiated species in the *Drosophila melanogaster* group (Coyne, et al., 1994). These results may indicate that very different evolutionary forces have come into play in shaping the genetic architecture of sexual isolation within versus between species, thus leaving these strikingly different genetic signatures. An alternative explanation is that the genetic architecture of species differences, such as sexual isolation, does not show a fixed pattern, but rather varies dramatically as a function of divergence time even when the same evolutionary trait is examined.

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Forty populations of *Potentilla argentea* L. (sensu lato) from southern Sweden was investigated to determine the pattern of genetic variation. Since the diploid form of *Potentilla argentea* has been reported to produce seeds apomictically, we wanted, in particular, to know if the natural variation pattern indicates a purely asexual mode of reproduction in nature. Pie

The investigated populations were chosen to represent the diploid form of *Potentilla argentea*. Nevertheless, sympatry between diploid and hexaploid forms was found in fourteen out of forty sampled populations. Two samples contained only hexaploid plants and twenty-four only diploid plants. The ploidy level was determined by root-tip analysis or by morphological analysis of greenhouse grown plants.

The mean number of leaves was higher in hexaploid than in diploid offspring plants grown in the greenhouse. Also the size of the largest leaf was greater in hexaploid than in diploid plants. Among the diploids, significant variation was found for both of these traits between populations as well as within populations.

The rate of germination of seeds from bagged flowers was, in general, higher among diploid than among hexaploid plants. The variability both between and within diploid populations was, however, considerable with respect to this trait.

Genetic variation was also detected with the RAPD method. To work, the method required a number of modifications of the standard protocol for DNA-purification, but it gave then clear and reproducible results. There were diagnostic band differences for some primers between hexaploid and diploid plants. The genetic variation detected in diploid *Potentilla argentea* was spread evenly both within and between the investigated populations. The detected level of variation was comparable to the level found in other investigated selfing plants, but the pattern of variation was more as expected from an outbreeding plant.

The general conclusion drawn is that *Potentilla argentea* may well have a variable breeding system. In nature, it does not, however, act in a predominantly asexual manner.

Genetic variation in *Potentilla argentea* L. (s.l.) in Southern Sweden
Holm S & Bengtsson BO

Distribution of transposable elements along the polytene chromosomes of *Drosophila melanogaster*. Test of the ectopic recombination model for maintenance of insertion site number.

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Data of chromosomal insertion site localization of various transposable elements (TEs) determined by *in situ* hybridization to the polytene chromosomes of *Drosophila melanogaster* were extracted from the literature. The data were from natural and laboratory populations, and concerned the transposons P and hobo, the retroposon I, the retrotransposons copia, mdg1, mdg3, 412, 297 and roo. We analyzed the distribution of the insertion sites along the chromosomes and searched for any relationships with relative DNA content and recombination rate. We show that transposable element insertion site number per chromosomal division was significantly correlated with the amount of DNA, estimated either by Sorsa (estimation based on chromosomal bands) or Bolshakov (estimation based on radioactive nucleotide incorporation criteria). The number of insertion sites weighted by DNA content appeared then not correlate with recombination rate for all TEs except hobo for which a positive correlation was detected. Contrary to suggestions in recent publications (see Charlesworth *et al.*, 1994), a possible dominant deleterious effect of chromosomal rearrangements due to recombination between TE insertions is thus not the main factor explaining the dynamics of transposable elements, since this hypothesis postulates a negative relationship between transposable element insertion site number and recombination rate.

Charlesworth, B., Sniegowski, P. & Stephan, W. (1994). The evolutionary dynamics of repetitive DNA in eukaryotes. *Nature* 371, 215-220.

SELECTION ON FEMALE PHENOTYPIC QUALITY IN THE GREAT TIT

In clarifying the role of optimization and constraints in life-history evolution, the concept of selection on environmental variance of traits has attracted a considerable interest recently. In birds, individuals laying early (and/or) large clutches may be fittest because directional selection operates on a correlated, environmentally determined trait (individuals' phenotypic quality, health, condition, nutritional state). It is also possible that selection acts on individuals' phenotypic quality independently of breeding traits. Detection of the true targets of selection therefore requires independent measurements for individuals phenotypic quality.

A long-term study of Great Tits (a small hole-nesting passerine) in south-east Estonia revealed that female's mean egg size is a good indicator of her phenotypic quality. Individuals laying large eggs were relatively heavier than others about one month after the onset of laying, indicating that clutch mean egg size reflects some persistent component of female condition. Females with large eggs recruited consistently more offspring to the breeding population. At that, mean egg size was not related to occurrence of embryonal or nestling mortality, suggesting that individuals laying large eggs were fittest because they provided better parental care.

High offspring fitness of females laying large eggs was independent on clutch size and laying date. Selection on clutch size revealed no consistent pattern over years, while there was weak directional selection for early laying. However, the effect of early laying on recruitment rate disappeared when egg size was incorporated into the model, indicating that laying date and egg size both reflect the same component of phenotypic quality of females, related to their ability to rear viable offspring. The latter suggests that the true target of selection was the phenotypic quality of female, not advanced laying *per se*.

MUTATIONAL PROCESSES IN NONGROWING CELLS OF *PSEUDOMONAS PUTIDA* UNDER STRESS CONDITIONS.

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In 7 years since the original paper by Cairns et al. (1988), the phenomenon called "adaptive mutation has been stimulated scientific debate whether certain mutations in bacteria occur at high frequency when their effects are beneficial. Under starvation cell division is repressed, still mutant crossing starvation continue to appear several days after plating onto selective media. The phenomenon of adaptive mutations has been described mostly in *Escherichia coli*. The difference in the spectrum of *lacZ* frameshift mutations were shown by Foster and Trimarchi (1994) as Rosenberg et al. (1994) when they compared the *lacZ* sequences of Lac⁺ revertants obtained during exponential growth with those for revertants obtained during starvation on lactose minimal plate

We used promoterless phenol degradation genes *pheBA* (encode for catechol 1,2-dioxygenase and phenol monooxygenase, respectively) as a reporter genes to isolate and characterize promoter mutations accumulating under selective pressure in *Pseudomonas putida*. We selected *Pseudomonas putida* strain PaW85, carrying promoterless phenol degradation genes, for growth on phenol minimal plates. After 2-5 days of incubation Phe⁺ clones were accumulated where transcription of the phenol degradation genes was activated due to generation of constitutive expressed σ^{70} -recognized promoters. These promoters were created as a result of transposition of Tn3 type transposon Tn4652 (the fusion promoters were formed at the junctions between terminal sequences of the inverted repeats of Tn4652 and sequences which flanked the inserted transposon point mutations and deletions. One base substitution C to A was prevailing over others (it occurred on 41 cases out of 54 investigated) when we studied DNA rearrangements other than transposition of Tn4652. The spectrum of mutations characterized in our case was same in both exponentially growing and starving cells. Comparative studies revealed that 24 Phe⁺ clones out of 29 before plating existing mutants (isolated on the second day of plating) and 25 Phe⁺ clones out of 26 postplating clones (fifth day), contained same base substitution C to A. We found that starvation itself did not increase accumulation of the Phe⁺ mutants. However, the number of postplating mutants accumulated on phenol minimal plates was dependent on the physiological state of the culture before plating.

References:

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Spatial Patterns of Genetic Variation Generated by Different Forms of Dispersal
During Range Expansion.

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Taking dispersal as the movement of individuals across the boundaries of populations defined by genetic discontinuities (demes), we examined the impact of three forms of dispersal, stepping-stone, normal and leptokurtic, on spatial genetic structure of expanding populations using computer simulations. When dispersal beyond neighbouring demes is allowed, rare long distance migration leads to the establishment of pocket populations in advance of the main invasion front and results in spatial clustering of genotypes which persist for hundreds of generations. Patchiness is more pronounced when dispersal is leptokurtic as is the case in many animal and plant species. We also show analytical results on the rate of decay of patchiness that arises from colonisation processes. These results are of particular interest because population genetic parameters such as gene flow and effective population size are commonly estimated using gene frequency divergence information assuming equilibrium conditions and island models. We show how the three forms of dispersal during colonisation bring about contrasting population genetic structures and how this affects estimates of gene flow. The implication to experimental studies of the spatial dimension of population genetic structure are discussed.

The effect of delayed population growth on the genetic differentiation of local populations subject to frequent extinctions and recolonizations

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The effects of delayed population growth on the genetic differentiation among populations subjected to local extinction and recolonization is investigated. It is shown that the addition of a prolonged period of population growth is to make the conditions for enhanced differentiation between local populations less restrictive and also to inflate the actual levels of differentiation. The effect is dependent on the relative magnitudes of k the number of colonizers and $2Nm$, twice the number of migrants between populations (Slatkin, 1977; Wade & McCauley, 1988), but also on r . In contrast to the earlier results the effects are also strongly influenced by the extinction rate, e . A generalization of the condition derived in Wade & McCauley (1988) is developed that take both extinction rate and growth rate into account. This condition is shown to boil down to a simple relationship between the average population size in the growing population, measured by the harmonic mean, and twice the normal migration rates among populations at equilibrium densities. The effect of a prolonged period of growth is strongest for relatively small and biologically reasonable extinction rates ($0.001 < e < 0.05$). As the extinction rate is increased the genetic differentiation becomes more and more influenced by properties of the founding group, such as founding size in relation to normal migration rates. Consequences of a variable extinction rate is discussed. It is shown that temporal variation in the extinction rate may sometimes shift a system from a situation where local extinction acts to reduces the genetic differentiation among local populations to a situation to where the genetic differentiation is enhanced or vice versa.

A contact zone with noncoincident clines for mitochondrial DNA and Y chromosome markers in the field vole (*Microtus agrestis*).

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Field voles (*Microtus agrestis*) from southern Sweden provide an excellent model system for examination of the behaviour of sex-specific genetic markers in contact zones. The Lund (Lu-) population in south-western Sweden is characterized by unique markers in mitochondrial DNA (mtDNA) as well as the Y chromosome. We examined a transect in the contact zone between the Lu-population and a standard (St-) population using the two genetic markers. The mtDNA and Y chromosome clines display a remarkable lack of coincidence, rarely observed in contact zones. The cline width for both markers is about 50 km, but the two clines are displaced from each other: the mtDNA cline is found in the central part of the study area, whereas the cline for the Y chromosome is located in the eastern part. Thus, the absolute width of the Lu-St zone spans about 95-110 km. As a result of the cline shift, all male hybrids carry the Lu-Y chromosome and St-type mtDNA. The other possible male hybrid class is lacking. The distinct noncoincidence of the mtDNA and Y chromosome clines is most likely explained by selection against male hybrids with the St-Y chromosome and Lu-mtDNA. It is possible that incompatibilities between the maternal genome of Lu-type animals and the paternal genome of St-type individuals exist. However, alternative explanations based on neutrality or selective advantage cannot be totally dismissed.

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PHENOTYPIC PLASTICITY AND CARRY-OVER EFFECTS

Carry-over effects, the lingering of induced phenotypic states for more than a single generation, are usually not treated as evolutionary adaptations. However, analytical results and computer simulations comparing different response strategies show that carry-over effects can have an advantage in some types of fluctuating environments. We argue that persistent phenotypic states that last for several, but not very many generations represent an adaptive mechanism on the ecological time scale intermediate between short-term individual adaptations and long-term evolutionary adaptations. This intermediate-term adaptation may be treated as a plastic response that is extended over several generations.

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Host related genetic differences between endoparasitoid populations.

Populations of the endoparasitoid *Ageniaspis fuscicollis* (Dalman) (Encyrtidae, Hymenoptera) reared from five host species, viz. *Yponomeuta cagnagellus*, *Y. evonymellus*, *Y. malinellus*, *Y. padellus* and *Y. rorellus* (Lepidoptera, Yponomeutidae) have been analysed using

- 1) allozyme electrophoresis and
- 2) PCR with single decamer primers of random sequence (Random Amplified Polymorphic DNA, RAPD).

Twenty-nine enzyme stainings revealed 42 putative loci, but only two polymorphic allozyme loci were found. *A. fuscicollis* populations reared from *Yponomeuta evonymellus* showed a higher frequency for the second most common allele at the Glucose phosphate isomerase (*Gpi*) locus than found in all other host populations. Moreover a host specific allele at the Phosphoglucumutase (*Pgm*) locus was found in populations parasitizing *Y. evonymellus*. A RAPD-polymorphism that proved to be codominant showed also a higher frequency for a second most common allele for *A. fuscicollis* populations parasitizing *Y. evonymellus*.

Analysis of the allele frequencies with *F*-statistics and estimation of levels of gene flow show a limited gene exchange between *A. fuscicollis* on *Y. evonymellus* and on other host populations. This pattern could be indicative for the existence of a host race. Host races are considered as the initial stage of sympatric speciation.

Other explanations, such as a sampling error can be excluded. Furthermore, for *A. fuscicollis* nothing is known about differences in the ability of the different genotypes to survive on a certain host species (host-specific selection).

Finally, the occurrence of female biased populations sampled from *Y. evonymellus* may cause the higher genetic diversity of these populations. A haplo-diploid species like *A. fuscicollis* possesses more alleles in a female biased population than in a di- / diploid population with the same number of individuals and may therefore contain a higher amount of genetic diversity.

The aminoacylation of a particular tRNA is the net result of two types of interactions, the productive (or positive) interaction with the cognate aminoacyl-tRNA synthetase and the nonproductive (or negative) interaction of the tRNA with the 19 noncognate synthetases. The term tRNA identity refers to this aminoacylation specificity. Recent techniques for structural comparison of tRNAs have advanced to the level where the specificity determinants - a small number of nucleotides, comprising the major identity elements in a tRNA molecule - can be evaluated. The goal is to complete a catalog of the identity elements for all 20 tRNA's. However, because of the enormous number of possible alternative combinations the testing by laboratory methods is strongly restricted. On the other hand the results of tRNA identity conversion experiments reveal that the statistical sequence similarity is not always connected "linearly" with the rate of function activity. For example, it is known that tRNAs that are quite similar in sequence may be charged with different amino acids, whereas iso-acceptor tRNAs can be quite dissimilar from each other. These and analogous facts raise a principal question concerning the reconstruction of adequate function or phylogenetic relationships on the basis of sequence *similarity*. In the proposed mathematical logical model the primary sequence information is represented as a combinational network. The goal of the analysis is to evaluate the "hidden" logical structure of functional interconnections considering the positional information of the nucleotide bases. An arbitrary L -length nucleotide amino acid sequence (where $L \leq 2^n$) with m symbol classes can be defined as a system of Boolean functions of n variables. By optimised function realisation (decomposition and synthesis) these interconnections can be expressed in algebraical, matrix or graphical forms. During the logical partitioning process some function values become distinguished in a canonical (or unique) way. These function values represent a set of elements in corresponding regions of the given tRNA. The sensitivity of the method for differentiating between topologies was tested on results of known tRNA identity conversion experiments. The found sets of *negative* and *positive* identity elements corresponded well to the laboratory results. E.g., in case of identity conversion from E.coli tRNA^{Phe} to tRNA^{Ala} the distinguished role of the G3-U70 "wobble" base-pair alteration shown on the basis of corresponding algebraic expressions and Hasse graphs. The consequences of individual or additive nucleotide alterations are illustrated on a point map. The method was tested also on E.coli tRNA's (including iso-acceptors) for reconstruction of phylogenetic relationships.

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Phenotypic Plasticity of Development Time and Body Size in *Drosophila melanogaster*.

A genetic cline in larval development time and body size in twenty *Drosophila melanogaster* populations collected from a 2600 km long north-south transect in the eastern coast of Australia is described. Flies from cooler areas are faster developing and eclose as larger adults than those from warmer areas. Six populations were picked from the transect to investigate phenotypic plasticity with temperature of development time and body size. Flies were raised at constant density, and at 14°, 18°, 21°, 25° and 29°C. At colder temperatures development was slower but adults eclosed at a larger size, the opposite of the evolutionary relationship between these two traits. Evolution in cooler climates produce flies that are faster developing irrespective of the rearing temperature. Among populations there was genetic variation for plasticity in body size. The relevance of these results in terms of thermal selection in natural populations of *D. melanogaster* will be discussed.

DNA sequence conservation in evolution is evidence for the functionality of sequence. However, sequence changes are consistent either with a lack of function or with adaptive substitution. McDonald and Kreitman have produced a test in which polymorphic variability and fixed substitutions in amino acid replacement and synonymous sites can give evidence for adaptive substitutions. Here we apply this test to variability in non-coding DNA in which the dichotomy between bases known to bind transcription factors and bases not known to bind such factors is substituted for the dichotomy between amino acid and synonymous sites. Data on the proximal part of the 'zebra' sequence of the pair rule fushi tarazu gene in the Drosophila melanogaster species group give weakly significant evidence for adaptive substitution in the region. Conditions required for the appropriate use of the test will be discussed.

Structural Divergence of Chromosomes and Its Effects Upon Meiosis

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Meiosis in most normal diploid species relies upon the pairing, synapsis and recombination of pairs of chromosomes with the same morphology and collinear genetic loci. This complementarity between homologues and the availability of only strictly homologous pairing partners ensure that meiosis proceeds in an orderly and regular manner. However, in diploid interspecific hybrids and allopolyploids, in which there is a structural divergence of chromosomes associated with speciation, the integrity of meiosis may be challenged. In diploid hybrids meiosis may be compromised by the association of chromosomes which are only similar to one another, or homoeologous. As an example, this paper refers to an interspecific hybrid of *Lolium*, which shows a remarkable capacity to accommodate structural differences during meiosis. Meiosis in allopolyploids is complicated by the potential at least for both homologous and homoeologous chromosome interaction. As a consequence, such organisms run the risk at best of dissipating any advantage gained by their hybrid condition, or at worst of segregating chromosomes at anaphase I in an irregular manner. This paper describes how several allopolyploids circumvent these problems by confining chiasmate association to strictly homologous chromosomes.

Genetic and reproductive dynamics of a semispecies hybrid zone in *Heliconius* butterflies (Nymphalidae: Lepidoptera)

Jiggins C, O McMillan & Mallet J

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Some of the more unusual hybrid zone case studies concern *Heliconius* butterflies where steep clines between colour pattern races are maintained by frequency dependent selection acting directly on colour pattern differences. Here we present results from a *Heliconius* hybrid zone where hybrids are very much rarer than would be expected under free gene flow. The forms are therefore considered as 'semispecies' rather than races. The cline is much steeper than in interracial hybrid zones and correlates well with a habitat transition. Allozyme data shows that there are considerable allelic differences between the forms and that introgression across the contact zone is negligible. Laboratory experiments suggest the deficit of hybrids is due to strong patterns of assortative mating, in the absence of any significant hybrid inviability or sterility. The implications of these results are discussed in terms of maintenance of the cline and for speciation within the group.

PARASITES, SEX AND EARLY REPRODUCTION IN A MIXED POPULATION OF
FRESHWATER SNAILS

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Two hypotheses have been presented on the role of castrating trematode parasites in the life history evolution of their hosts. First, high risk of infection is predicted to select for sexual reproduction because genetically variable offspring should be less vulnerable to parasites specializing on common genotypes [Lively, C. M. *Evol.* 46, 907-913 (1992), Howard, R. S. & Lively, C. M. *Nature* 367, 554-557 (1994)]. Second, life-history theory predicts that high infection risk selects for earlier reproduction, smaller size at reproduction and higher reproductive effort [Gadgil, M. & Bossert, W. H. *Am. Nat.* 104, 1-24 (1970), Law, R. *Am. Nat.* 114, 399-417 (1979), Michod, R. E. *Am. Nat.* 113, 531-550 (1979), Lafferty, K. D. *Oikos* 68(1), 3-11 (1993)].

We present results of a field study supporting both hypotheses. In a collection of samples of freshwater snail *Potamopyrgus antipodarum* from Lake Alexandrina, New Zealand, the proportion of males was positively correlated and size of brooding females was negatively correlated with parasite prevalence when corrected for the mean length of the snails in the sample. The result also suggest that evolutionary response to parasites may take place in a relatively small scale, in this case within a lake, or even within the habitat. This is in accordance with the predictions of the hypotheses and emphasizes the role of castrating parasites in the evolution of snail life histories.

Multiple displays in animal communication

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Why are animal displays so complex? In contexts ranging from courtship and mating to parent-offspring communication to predator deterrence, biological signals often involve a number of different visual, auditory and/or olfactory components. Previous models of communication have tended to ignore this complexity, assuming that only one kind of display is available. Here, a new game-theoretical model of signalling is described, in which signallers may use more than one display to advertise their qualities. Additional displays may serve to enhance the accuracy with which receivers assess a single quality (the 'backup signal' hypothesis), or to provide information about different qualities (the 'multiple message' hypothesis). Multiple signals are shown to be stable, even when multiple receiver preferences entail significant costs, provided that signalling costs are strongly accelerating. In such cases, signallers bias their investment towards more efficient forms of signal, but not to the exclusion of other display types. When costs are not strongly accelerating, by contrast, individual signallers employ only a single display at equilibrium. If different signals provide information about different qualities, however, then the equilibrium may feature alternative signalling strategies, with signallers who excel in one quality employing one kind of display, and those who excel in another quality employing another kind.

Molecular characterization of the Bulinus forskalii group (Gastropoda: Planorbidae) in Cameroon, West Africa; intermediate hosts for Schistosoma spp.

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The morphological definition of taxa at the species-level has proven difficult within the Bulinus forskalii group. For instance, B. forskalii, and B. senegalensis are closely related, conchologically similar and often occur in the same population, yet transmit different schistosome species. Low stringency PCR DNA profiling was used to examine genetic variation among B. forskalii, B. senegalensis, and B. camerunensis recently collected from Cameroon. Each one of the three species can be clearly differentiated from its congeners by its DNA profile. Prior to analysis of data by phylogenetic methods, fragments apparently shared between taxa were tested for homology, by excising and radiolabelling them for use as probes. Phylogenetic analyses suggests B. forskalii and B. senegalensis form distinct branches, with B. camerunensis as a sister group to B. forskalii. To obtain for reproducible results between laboratories and negate ambiguities in scoring the DNA profiles, taxon-specific primers and probes are currently being designed by cloning and sequencing the diagnostic PCR fragments to provide a simple field identification system.

The consequences of pre- and postbreeding costs of reproduction on the evolution of reproductive effort tactics.

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The evolutionary consequences of costs of reproduction are usually evaluated in terms of postbreeding survival and fecundity costs. Such demographic costs may follow as, for example, a female drains her somatic resources into reproduction. However, some reproductive tactics may lead to costs of reproduction that are expressed in terms of prebreeding survival.

We present an optimality model where total absolute effort may originate from two different components. The first component, *accumulation effort*, measures the amount of resources that the female accumulates for reproduction during the prebreeding period. The second component, *somatic effort*, represents the amount of resources drained from somatic demands relative to non-reproductive individuals. We focus on the case where accumulation effort implies costs on prebreeding survival and somatic effort implies costs on postbreeding survival. Effective fecundity is assumed to be a function of both components.

We solve for optimal tactics by maximizing fitness over a single breeding season, assuming a constant total investment in reproduction. Our analysis suggests that the evolution of accumulation effort requires that marginal prebreeding costs due to accumulated resources remain low relative to marginal postbreeding costs implied by somatic effort. We also allow the constraint to vary and show that when the total investment in reproduction increases, optimal somatic effort increases relative to optimal accumulation effort.

We suggest that the temporal distribution of reproductive costs may have an important impact on the evolution of reproductive effort tactics, and emphasize the need of empirical studies evaluating the occurrence and consequences of prebreeding costs of reproduction. Natural selection may well favour different effort tactics for satisfying the energy demands of reproduction, some of which may involve optimization of the balance between pre- and postbreeding costs of reproduction. For organisms relying on tactics implying prebreeding costs, empirical studies monitoring postbreeding survival only may not reveal the major cost of reproduction.

Preserving Genes: the Maintenance of Genetic Variation in a Model Metapopulation

Olivia Judson

Understanding how genetic variability is maintained in natural populations is of both theoretical and practical interest. In particular, the subdivision of populations into demes linked by low levels of migration has been suggested to play an important role. But the maintenance of genetic variation in populations is also often linked to the maintenance of sexual reproduction: any force that acts to maintain sex should also act to maintain variation. One theory for the maintenance of sex, the Red Queen, states that sex and variation are maintained by antagonistic coevolutionary interactions—especially those between hosts and their harmful parasites—that give rise to negative frequency-dependent selection. In this paper I present a model to examine the relationships between population subdivision, negative frequency-dependent selection due to parasites, the maintenance of sex, and the preservation of alleles from fixation. The results show strong interactions between migration rates, negative frequency-dependent selection, and the maintenance of variability for sexual and asexual populations.

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**Genetic variation of sympatric and allopatric populations of
hybridizing freshwater snail species**

Because of incomplete reproductive isolation, genetically and morphologically differentiated species sometimes hybridize in nature. Subsequent introgression may affect the whole evolutionary processes including speciation and phylogenetic relationships. Allozyme data from Lake Garda, Italy are consistent with the hypothesis of gene introgression from *Viviparus ater* into *V. contectus* and vice versa. First generation hybrids were collected in nature and their hybrid status was confirmed by allozyme markers. The frequency of F_1 hybrids was as high as 0.7 % in nature. In order to test whether presumably introgressed alleles are missing from allopatric populations, we extended our genetic studies to allopatric and sympatric populations from other areas of central Europe.

The six allozyme loci which were informative in Lake Garda, Italy were analyzed from nine sympatric populations and four allopatric populations each, of *Viviparus ater* and *V. contectus*. A total of 900 newly collected snails from Italy, Switzerland, and Germany was examined electrophoretically. *V. ater* had low genetic variation (the jackknifed mean of Wright's $F_{ST} \pm S.E.$ over four loci was 0.041 ± 0.004), and *contectus*-like alleles were found at low frequencies in both allopatric and sympatric populations. On the other hand, *V. contectus* showed high genetic differentiation especially at four loci (the jackknifed mean of $F_{ST} \pm S.E.$ over six loci was 0.546 ± 0.166). Sympatric populations of *V. contectus* in Lake Como, Italy possessed only *ater*-like alleles at one pair of linked loci. These concordant substitutions may be due to historical introgression. Besides these substitutions, no clear differences between allopatric and sympatric populations were observed. These results indicate that allelic substitution rates are high in *V. contectus*. The high substitution rates can be obtained by high mutation rates, introgression, or small population sizes.

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Published models of sympatric speciation require the existence of a protected polymorphism, such that alleles advantageous in one habitat and deleterious in the other habitat are maintained by selection. The presence of such polymorphism favours habitat fidelity, habitat choice, and assortative mating. However, the conditions for maintenance of such polymorphism are rather stringent.

I suggest that mutations constitute a complementary factor that promotes sympatric speciation if the magnitude of their effects on fitness differs between habitats. Simple genetic models suggest that such mutations favour the evolution of habitat fidelity and assortative mating with respect to the habitat, thus leading to formation of "habitat races", which may be viewed as incipient sympatric speciation. The mechanism I propose works both for deleterious mutations, opposed by selection but constantly replenished by the mutation process, and for advantageous mutations that arise occasionally and spread to fixation. Beneficial mutations with host-specific effects could be particularly important in promoting sympatric speciation in parasites and herbivorous arthropods, in which the postulated coevolutionary arms races with their hosts involve constant incorporation of new mutations into gene pools.

THE EVOLUTION OF PARTITIONING OF REPRODUCTION IN ANIMAL SOCIETIES

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IT 8.

173.

The dynamics of social groups are determined by a balance between cooperation and conflict among group members. One of the major source of conflict relates to the apportionment of reproduction among individuals. There is tremendous intra- and interspecific variation in reproductive skew, with some societies where all individuals reproduce equally and some others where a single individual completely monopolizes reproduction.

Models of the evolution of reproductive skew have analysed how genetic relatedness of potential breeders, relative fighting abilities of these individuals, ecological constraints on solitary founding, and productivity advantages of peaceful associations should influence the stable reproductive skew of animal societies. The magnitude of reproductive skew is predicted to increase with increasing ecological constraints on independent breeding, because subordinates can expect only small payoffs for leaving if ecological conditions are harsh. Reproductive skew is also predicted to increase with increased relatedness among queens because subordinates that are more closely related to dominants automatically receive larger kin-selective benefits for cooperating peacefully with dominants, hence they require smaller direct reproductive inducements for such cooperation.

At present, few studies have conducted detailed tests of the skew models, but the available data are consistent with the predictions. For example, high skew is almost invariably associated with high relatedness among group-members, and a positive relationship between the degree of skew and relatedness among group members has been described in several wasp, and mammal species. As predicted by the models, the degree of reproductive skew also apparently increases with greater ecological constraints on dispersal in several wasp, ant, bird and mammal species. Finally, as assumed by the optimal skew models subordinates apparently can detect reproductive 'cheating' by the dominant, becoming aggressive if their amount of reproduction falls below some minimal value in *Polistes* paper wasps.

A further predictions of the skew models is that skews in mother-daughter associations (asymmetrical relatedness) will tend to be greater than those in sibling associations (symmetrical relatedness) even when breeders in each kind of association have the same relatedness. Data from wasp and bird societies again are consistent with this prediction. A general message emerging from these data is that the same ecological factors together with internal factors such as relatedness, determine the degree of within-group conflict, partitioning of reproduction and stable reproductive structure in animals, independently of whether they are insects, birds or mammals.

Evolution of *SRY* in the Felidae

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SRY is the Y-located gene required for testis determination. The protein that it encodes contains N and C terminal regions flanking an HMG box, which has been shown to have DNA binding and bending activity. Comparisons of the human and mouse proteins have revealed that the HMG box region is conserved between species, while contrary to expectation, the flanking N and C terminal ones are not. All three regions have been examined in studies which compared sequences from closely related species, in one case from primates and in the other from Old World mice and rats; those studies found that *SRY* is evolving rapidly in the regions flanking the HMG box, as indicated by a high ratio of non-synonymous changes per non-synonymous site to synonymous changes per synonymous site (K_a/K_s). The rapid evolution of parts of *SRY* suggests either that those regions are functionally unconstrained or that they are functional and subject to selection for change in sequence. As previous comparative sequence analyses were limited by the small number of species compared, we have undertaken an investigation of *SRY* in the 37 members of the family Felidae. Not only does this group have a well-defined phylogeny, but the individual species within it have well-characterised mating structures, allowing us to test hypotheses which seek to explain the rapid evolution of *SRY*. To date, we have completed the sequencing of *SRY* from more than 10 of the species, including members of each of the three main lineages, the *Panthera*, the domestic cats, and the ocelots.

FUNCTIONAL ORGANIZATION OF MOUSE CENTROMERES: IMPLICATIONS FOR EVOLUTION

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T 1.3

The relationship between the primary DNA sequence and biological function (chromosome segregation) of the mammalian centromere remains poorly understood. Variation in centromeric sequence between species contrasts sharply with apparent conservation of the biological function, as evidenced by somatic cell hybrids.

This puzzle is illustrated by the Asian mouse *Mus caroli*. It does not contain the centromeric minor satellite DNA family, the best candidate for a functional centromeric sequence in *M. musculus*. However, a novel centromeric satellite cloned from *M. caroli* contains a variant but functional binding site for the centromere-associated protein CENP-B. Conservation of CENP-B binding capacity in the face of satellite sequence evolution will be discussed.

M. spretus does contain minor satellite, but it is heavily amplified and distributed throughout a large domain of pericentric heterochromatin. Centromere-associated proteins such as CENP-B localise to a sub-region of this heterochromatic domain. Evidence will be presented that this reflects an epigenetic restriction of centromere positioning caused by DNA methylation. The implications of epigenetic regulation of centromere function in karyotype evolution will be discussed.

176a

T8

Evolution of mating preferences for male genetic quality
Kirkpatrick M

Female preferences have caused the evolution of extreme male mating displays throughout the animal kingdom. One important but controversial class of hypotheses for the evolution of these preferences involves "indirect selection". Even in the absence of direct fitness effects, preference for males with high overall fitness can spread via a genetic correlation that develops naturally between preference and fitness alleles. A quantitative expression for the force of indirect selection is presented that applies to any female mating behavior, is relatively insensitive to the underlying genetics, and is based on measurable quantities:

$$\frac{\Delta \bar{P}}{\sigma_P} = \frac{1}{2} \rho_{PT} r_{Tw} h_T h_P^2 \sqrt{C_w}.$$

In conjunction with the limited data now available, this and further results suggest that the evolutionary forces generated by indirect selection on preferences are weak.

Plasticity: what is it, and what is it good for?

Kirkpatrick M 177

IT

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The linkage between genotypes and phenotypes is modified by development, physiology, and behavior. How closely do the reaction norms that we see match the ones that selection favors? This fundamental question about plasticity can be probed using experimental intervention, arguments from design, and direct measurements of selection. I review these approaches, and suggest that they are all needed to progress from our current qualitative understanding of plasticity to a quantitative one.

Indicators for biotope management: Analyses of the Cynipid *Isocolus scabiosae* galling different host plant structures

P3

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In calcareous grassland biotopes the gall wasp *Isocolus scabiosae* (Cynipidae, Cynipinae, Aulacini) is known as a monophagous gall former of the knapweed *Centaurea scabiosa*. Their galls normally occur at host plant shoots. But in the Eifel region in Germany root-galls induced at bottomlevel were also detected. Emerging individuals of such a root-gall-population and two adjacent shoot-gall-populations were compared. Showing no morphometric differences standard horizontal electrophoresis with cellulose-acetate gels was used. Out of the ten regularly scored loci five were polymorphic with two alleles each. No heterozygous individual was found at either locus. A fixed allele difference was found in locus GPDH2. All root-gall-individuals shared the slow allele whereas all shoot-gall-individuals shared the fast one. As in both groups males and females were mixed and populations consisted of several galls the difference is not linked to sex or close relationship of wasps within a single gall. Due to very high parasitism only one root-gall-population could be considered, but some single wasps out of root galls from three other sites in the region are characterized by the slow GPDH2 allele too. Thus within the species the two genotypes are specialized to quite different plant structures for galling. For this they are expected to have different phenology also raising questions of adaptation and sympatric speciation.

But both types are affected differently by mowing or sheep-grazing of calcareous grasslands in autumn. These are the dominant conservation management measures in this region. As the univoltin gallwasps hibernate as pupae inside the galls mainly shoot-gall-individuals are destroyed whereas root-gall-individuals may survive. This is an example that nature conservation measures may not only reduce number but also genetic diversity of typical biotopeconnected populations.

The evolution of simple population dynamics

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We investigated the evolution of demographic parameters determining the dynamics of density-dependent population growth with simulations of a growth model proposed by Maynard Smith and Slatkin. In particular, we considered whether the dynamics behavior will evolve to stability or chaos. When the three parameters - equilibrium density, growth rate and complexity - were not constrained by trade-offs, the dynamics rapidly evolved to stability. Once stability was attained, the strongest selection pressure was for increasing equilibrium density, while complexity drifted into the region coding for more stability. Most constraints changed these conclusions only qualitatively. For example, if equilibrium density was positively associated with complexity, populations with a bounded equilibrium density still evolved towards stability. The opposing selection pressures for increased equilibrium density and for reduced complexity led the population to be maintained on the edge of stability. The only case we found that did not evolve to stability was a positive association between equilibrium density and complexity together with a bounded growth rate. In this case, the level of complexity depended on the maximum growth rate, and it was possible that chaotic population dynamics evolved. Nevertheless, the overall tendency for the populations to evolve to stability was striking.

Inbreeding depression in *Scots Pine*: the later life stages.

P5

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The deleterious effects of inbreeding in the early life stages of *Scots Pine* have been well documented. Selfing is accompanied by a low seed set caused by the expression of highly deleterious alleles (lethals). Virtually nothing is known, however, about the later life stages. Inbreeding depression in these stages will be caused by mildly deleterious alleles and the effects are expected to accumulate during the life cycle. We present preliminary results from an experiment which is now running for 25 years and documents the consequences of selfing during the later life stages of *Scots Pine*. Open pollinated (outcrossed) and selfed seedlings of different maternal trees were planted at experimental sites of the Punkaharju breeding station in Southern Finland and measured at 5-year intervals. To evaluate the consequences of planting density on the performance of the crosstypes, seedlings were planted in competitive (close spacing, *i.e.*, nearest neighbour is one metre away) and non-competitive conditions.

Geographic Variation of Mitochondrial DNA Restriction Fragments of Common Rats, Rattus norvegicus caraco Pallas(Rodentia, Mammalia), from Korea

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Samples of common rats(Rattus norvegicus caraco) from six localities in Korea were used for the analyses of mitochondrial DNA(mtDNA) fragment patterns resulted from the digestion with eight restriction enzymes.

A total of 39 fragments were recognized and eight mtDNA clones were revealed. Among 47 samples studied, 30 samples from five localities(26 from Cheongju, 1 from Boeun, 1 from Jochiwon, 1 from Mt. Deokyo, 1 from Seoul) were identical in their mtDNA genotypes. In addition, three samples from two localities(2 from Cheongju, 1 from Boeun) had the same mtDNA genotype.

The nucleotide-sequence divergences(p) among eight mtDNA clones ranged from 0.35% to 4.04%. Moreover, the eight clones were grouped into two major subgroups with the mean divergence value of 2.46%. One subgroup was composed of two clones(two samples from Goisan), and the other subgroup consisted of other six clones(45 samples from other five localities). The two subgroups were also distinct in their mtDNA genotypes of EcoR I and Stu I. Furthermore, the maximum divergence among common rats from Korea in this study is twice higher than that among common rats from the United States and Japan by Brown and Simpson(1981).

Further analyses with additional samples from Goisan and other localities appeared to be necessary in order to clarify the taxonomic status of the distinct mtDNA subgroups.

KEY WORDS: Systematics, mtDNA, Rattus norvegicus caraco, Korea.

Trade-off between litter size and offspring viability

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Introduction

One of the assumptions of life-history theory is the trade-off between the number and quality of offspring. We studied the existence of this trade-off in the bank vole *Clethrionomys glareolus*. In this species there is a large variation in litter size (2-9).

Material and methods

Live-trapped bank vole females and males were paired in the laboratory. Females were checked twice daily to determine the time of parturition and litter size. Pups were weighted at the age of one, six, twelve and 60 days. In September, at the mean age of 60 days, individuals were released to eight large outdoor enclosures (each 0.25 ha) to overwinter. The survival of individuals were monitored by live-trapping in the beginning of next breeding season in May.

Results

Number of offspring correlated negatively with the weight of pups (mean weight of pups in the litter) at the age of one day ($n = 25$, $r_s = -0.40$, $p < 0.05$). Weight of individuals at the age of one day also explained significantly the survival over winter, so that heavier pups were more likely to survive (Logistic regression, $n = 24$, $p < 0.05$).

Discussion

According to our results, there is a negative correlation between the number and weight of pups in the bank vole. The weight at birth seems to explain the overwintering possibilities to the following breeding season. Therefore, our results give evidence of the existence of a trade-off between litter size and offspring viability.

183.

ARTIODACTYL GENOME FINGERPRINTING BY SINE-PCR AND SSR-
ANCHORED-PCR

T2/

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We have used SINE-PCR and a related new technique, where simple sequence repeats (SSR, or microsatellites) are used as PCR primers, to fingerprint genomes of six artiodactyl species: cow and sheep (Bovidae), moose, white tailed deer and reindeer (Cervidae) and pig (Suidae). Average percent divergence values were estimated from banding patterns of SINEmorphs (SINEs) generated by five SINE primers and from SSR-anchored morphs (SSRs) generated by three combinations of SSR-anchored primers [(CA)_nAT, (CA)_nGG and (CA)_nAG]. Correlations of these values were estimated by matrix comparison analysis. Only one primer did not show very good correlations and it was not included to UPGMA clustering analysis. Both methods showed the same phylogenetic clustering of the species, but lower levels of divergence between and among families were observed with SINEs than with SSRs. The most similar species pair among the six species studied was the taxonomically most related one, white-tailed deer and reindeer. Bovidae species studied were more distantly related to each other than the Cervidae species, which was expected. The obvious general conclusion is that this kind of methods are reliable, as they provide taxonomically logical and constant results.

EFFECT OF THE MELANOTIC TUMOURS ON THE ADULT VIABILITY OF THEIR CARRIERS IN DROSOPHILA MELANOGASTER.

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Since Bridges(1916) reported the melanotic tumours in Drosophila melanogaster for the first time, a large number of melanotic tumourous strains have been reported. Kosuda(1989) found a new tumourous strain, C-104, in which melanotic tumours develop only in the adult stage, exclusively in the vicinity of female spermathecae. They very often envelope either or both spermathecae. It is generally accepted that the melanotic tumour is the result of the aggregation of blood cells accompanied by melanization. The aggregation of haemocytes, melanization and the subsequent encapsulation are considered to be a common nonself-recognition or defence reaction in insects.

In the present experiment, the incidence of melanotic tumour development was disclosed to be higher in the dead flies than in the live ones. The fact explicitly indicates the deleterious effect of the melanotic tumours on the adult viability of their carriers. This fact implies that non-self recognition or self-defense reaction is accomplished by paying some or less burdens to the organisms.

185. Sexual selection in a wolf spider: male drumming activity, body size and viability T8

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Females are often believed to actively choose viable males as mates, but this belief is relying only on some pieces of empirical evidence from birds. In my study I report active female choice for viable males in an invertebrate, a wolf spider *Hygrolycosa rubrofasciata*. I established trials where I observed female choice in relation to male courtship drumming activity and body size. Females chose the most actively drumming males as mating partners but the body size of the males did not seem to be selected. Male drumming activity turned out to be a good predictor of male viability while male viability was independent of male body mass. My results suggest that by actively choosing mates according to male drumming performance, but independently of male body mass, females are preferring viable males as mates. Since *H. rubrofasciata* males do not provide obvious direct benefits to their offspring, females may gain some indirect benefits; offspring may have higher chance of survival or the offspring may inherit the attractiveness of their father.

Molecular evolution of three fungal proteins. Vassiliki Koufopanou, Austin Burt and John Taylor. Department of Plant Biology, University of California, Berkeley.

The nature of selection acting on protein-coding loci can be inferred by a comparison of the ratio of replacement to synonymous substitutions of nucleic acids within and between species (1, 2, 3). A higher ratio between species than within indicates that species divergence represents adaptation to different environments (positive selection changing amino acids), while equal ratios within and between species suggest divergence by a random accumulation of mutations (neutral model). We have compared DNA sequence polymorphisms for three protein-coding genes (4-hydroxyphenyl-pyruvate dioxygenase, chitin synthase and orotidine 5-monophosphate decarboxylase), within and between three closely related species of ascomycete fungi: Coccidioides immitis, a human pathogen causing valley fever, and its closest relatives Uncinocarpus reesii and Auxarthron zuffianum (4, 5). When parsimony trees based on each gene are compared, different isolates group consistently within their respective species, indicating genetic isolation among the three species; within species, the trees are mostly congruent, suggesting only partial mixis among isolates. Nucleotide divergence between species varies between 15 and 39%, and amino acid divergence between 1.5 and 35%, indicating that the three genes and their proteins evolve at different rates. The amount of polymorphism within species is similar in all three genes (coding areas), ranging between 0.5 and 8%. Silent nucleotide divergence is similar in all three proteins, suggesting equal mutation rates among proteins, but large differences among proteins in replacement nucleotide divergence indicate that the proteins are subject to different constraints. Two of the genes (4-HPPD and CHS) have twice as many replacement mutations between species compared to within, suggesting adaptive evolution changing amino acids, but the differences are not statistically significant; a third gene (OMPD), has about equal ratios within and between species, consistent with the neutral model.

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RAPD MARKERS INDICATE THAT HORIZONTAL TRANSMISSION IS THE PREDOMINANT MODE OF TRANSMISSION IN ATKINSONELLA HYPOXYLON.

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The success of vertical and horizontal transmission modes was investigated in Atkinsonella hypoxylon using RAPD markers. Atkinsonella hypoxylon and other clavicipitaceous fungi, form a symbiotic continuum from mutualistic to pathogenic interactions with plant hosts. Horizontal transmission of A. hypoxylon is associated with the castration of Danthonia spicata's outcrossed flowers because the fungus fruiting body (where contagious spores are produced) develops in place of host's inflorescence. However, D. spicata can still reproduce through basal, obligately selfed, cleistogamous seeds that are infected with fungal hyphae. Although potential for vertical transmission is high (90% of cleistogamous seeds of infected plants carry fungal hyphae) and horizontal transmission has been rarely documented, the relative contributions of the two modes of transmission have never been quantified in this or related fungi.

Isolates from A. hypoxylon were genotyped with ten RAPD markers and pairwise linkage disequilibria were calculated. Of the 45 comparisons, only four were significant at $p < 0.05$, but none were significant at $p < 0.02$. These results indicate that the population sampled exists in Hardy-Weinberg equilibrium and that clonal reproduction by vertical transmission through seeds is not very successful. This fungal population is therefore maintained mainly through contagious spread by spores.

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A study of phenotypic variance of bilateral traits in fishes

The developmental instability (DI) and phenotypic variance (σ^2) for a few meristic bilateral characters has been studied along with character size (M) in 6 closely related fish species in a search for connection between the stochastic (σ_s^2) and factorial (σ_f^2) components of σ^2 (Kozhara, 1994). An evident negative correlation between the latter was discovered in most within-species comparisons that is consistent with well-known feedback displayed by heterozygosity and DI.

The result was opposite, however, in among-species and among-characters comparison, in spite of scaling out σ_s^2 -M and σ_f^2 -M dependences. This may prove M. Soule's assumption concerning decreased DI in traits under the stronger genetical control (1982) to be not universal. For all that, his expectations to have higher proportion of genetic variance for larger characters as against smaller ones seems to be confirmed by having found the σ_s^2/σ^2 ratio to increase with character size in the group of species/characters under consideration.

A.V. Kozhara, J. Appl. Ichthyol. 1994: N10, P. 167-181

M. Soule, Amer. Natur. 1982: V. 120, N6, P. 751-764

188 · Optimal allocation of resources explains Charnov's life history invariants for indeterminate growers

T1

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Using an optimal resource allocation model, Kozłowski and Weiner recently showed that interspecific allometries of physiological (respiration, assimilation and production rates) as well as life history (age and size at maturity, life expectancy) parameters are byproducts of body-size optimization in animals with determinate growth. Here I extend the analysis to animals with indeterminate growth, such as fish or reptiles. It is optimal for such organisms living in a seasonal environment to grow after maturation, although more resources should be devoted to reproduction year after year. This leads to growth curves that can be closely approximated by the Bertalanffy equation characterized by two parameters, that is, growth rate k and asymptotic length l_{∞} . Unlike in Charnov's model, this kind of growth curve is the result and not the assumption. Size at maturation l_a , asymptotic length l_{∞} , l_a/l_{∞} ratio, and growth parameter k are related to mortality rate, growing season length, and the parameters describing the dependence of production rate on body size, through optimal resource allocation to growth and reproduction. A larger fraction of growth is realized after maturation if mortality is heavy.

I generated sets of these parameters with a random number generator of normal distribution. Then the schedule of growth was calculated for each "species" obtained in this way, under the assumption of optimal allocation of resources. Interspecific comparisons in a set of such species resemble the empirical patterns discovered by Beverton and Holt and discussed extensively by Charnov (1993): l_a/l_{∞} is relatively constant, mortality rate and growth rate k are positively related, and asymptotic length and growth rate are negatively correlated. Season length strongly affects these relations, which may explain the well-known differences between local populations. If all the model parameters vary at random between species, the points are scattered around regression lines describing Beverton and Holt's patterns.

When we interpret these results, we must remember that the growth curves and the Bertalanffy equation parameters describing them are not subject to natural selection. These parameters, as all the relations between them and mortality rate and growing season length, are side-effects of optimal allocation of resources to growth and reproduction. Resemblance to patterns found among fish or reptiles supports the models of life history optimization based on resource allocation.

A NEW HYPOTHESIS ON THE EVOLUTION OF SEX DETERMINATION IN
VERTEBRATES; BIG FEMALES ZW, BIG MALES XY.

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All vertebrates have the capacity to develop as female or male depending on: (a) genetic sex determination (GSD), in which sex is determined at conception by genotype; and (b) environmental sex determination (ESD), in which sex is determined later in life by the influence of environmental variables. It is suggested that both types of sex determination act through the same mechanism: phenotypic variance for growth of the undifferentiated gonad, meaning that ESD and GSD only differ in the degree to which the environment contributes to this phenotypic variance. We propose a simple model in which GSD evolves from ESD when an allele that accelerates embryonal growth takes over the role of environment in bringing about differential growth. According to this model, species with ESD showing female size advantage are predisposed to evolve to female heterogamety, whereas species with male size advantage are predisposed to evolve to male heterogamety.

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HABITAT PREFERENCE AS A BARRIER TO GENE FLOW IN HYBRID ZONES

A hybrid zone characterised by narrow concordant clines implies that strong natural selection is counteracting migration and recombination, creating a barrier to gene flow. Using a model of heterozygote disadvantage, changes in allele frequency and the strength of pairwise linkage disequilibria measured across a zone give estimates of the strength of selection acting and the magnitude of the barrier to gene flow posed by this selection. However these analytical results depend on assumptions about both the strength and nature of selection. This study uses simulations to investigate how robust the estimates are to alterations in the assumptions; both epistasis or geographical selection gradient produce similar patterns to heterozygote disadvantage. Assumptions of weak selection are frequently violated, but with stronger selection coefficients agreement with predictions is still good.

Hybrid zones are a natural test of the fitness of blocks of co-adapted genes in comparison to that of those in a recombined mixture. However they also test the efficiency of behavioural isolating mechanisms in preventing gene flow. A genetically-determined preference for different breeding habitats in the parental populations will cause assortative mating, serving to isolate the taxa. Its effect is markedly stronger when selection acts against genes in the alternative habitat or geographic location than endogenously, against hybrid individuals. Clines are steepened, but care must be taken when calculating descriptive statistics. Cline shape will be affected by the respective availability of habitat types, so that even if selection is entirely endogenous the hybrid zone should be centred on an ecotone. The implications for inferences about the strength of selection and magnitude of the barrier to gene flow are discussed. For example, under habitat-dependent selection, a preference will generate greater linkage disequilibria than that expected with random mating.

These results help with interpretation of data on hybrid zones where complex behavioural and ecological factors interact with selection acting against hybrid individuals to create barriers to gene flow.

Diversification of endemic Nile Perch *Lates niloticus* (Centropomidae, Pisces) populations in Lake Tanganyika, East Africa, studied with RAPD-PCR

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Genetic differentiation of endemic Nile-perch *Lates niloticus* populations in Lake Tanganyika was studied using the DNA method RAPD-PCR (Random Amplified Polymorphic DNA). Identification of possible substocks is needed for the fisheries management planning.

A total of 217 alcohol stored samples from five localities during dry and rainy seasons were analysed using RAPD with three primers. The number of bands observed was 52. RAPD proved to be a suitable method for the analysis of Lake Tanganyika fish stocks.

The presence and absence of amplified DNA fragments was used to group individuals to breeding populations. Individuals were grouped using a similarity index and percentual index of matches and hierarchical clustering using furthest neighbor-joining (complete linkage) of SPSS. All clusterings were tested by discriminant analysis using Mahalanobis distance. The coherence of groups was maintained during all groupings.

Similarity of banding pattern of RAPD fragments in one group was over 87.2%. 18 of 52 DNA fragments were selecting between populations, being present on all members of one population and absent from all members of another population. Nei's genetic identity between populations varied from 0.650 to 0.905.

Lake Tanganyika is approximately 20 million years old. The age of diversification can be estimated by using the values of Nei's I reached by converting the RAPD data to allele frequencies for BIOSYS programme. If the diversification was stable, the origin of differentiation between the strains from Malagarazi and Chituta started 7 million years ago. The differentiation between Sumbu and Moba is almost as old. The number of selective fragments, that are present on all members of one population, and totally lack from another, is quite large between these populations (8 and 6). 7 million years ago, during Miocene, Lake Tanganyika consisted of small, mostly isolated lakes.

The studied samples of pelagic Nile Perch *Lates niloticus* from Lake Tanganyika represent seven genetically diversified populations. Six populations are geographically local, while members of seventh population were captured from wider area. Anyhow, there is no absolute evidence of a total reproductive isolation, as no conserved fragments were found. Conserved fragments are present on all members of one population, and not present on others.

Are random mutations the optimal way to change the DNA?

193.

T2

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The adaptive significance of different mutational processes is explored from a theoretical point of view. In the standard evolutionary asexual model, the genome of the offspring is an almost exact replica of the genome of the parent except for a constant, genome-wide, mutation rate caused by inaccuracies in the duplication. This mutation rate is often seen as emerging from inherent physical properties of the organism and its environment. The paper builds a mathematical framework under which one can ask whether inducing random point mutations is optimal for a certain set of environments. Constant, spontaneously changing, fluctuating and randomly changing environments are explored, and it is shown that for some environmental conditions random mutations are best, whereas for others different kinds of changes are optimal. The tools developed to address this question can also be used to gain insight into the role of sex in evolution. Applying the framework to sexually reproducing organisms, it is shown that in this case there are more efficient ways to change the genetic material than the best asexual methods, for certain environmental conditions.

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T4

Heavy metal tolerance in populations of *Calamagrostis epigejos* (L.) ROTH and *Agropyron repens* (L.) P. BEAUV

The grass species *Agropyron repens* and *Calamagrostis epigejos* are able to survive on heavy metal contaminated sites like in the vicinity of copper smelters. The aim of this study was to find out if those populations evolve heavy metal tolerance.

Plant and soil samples were taken from control sites, a moderately contaminated abandoned sewage farm, and two copper smelters in Poland. The soil samples were analysed regarding the contents of copper, zinc, lead and cadmium. The phytotoxic potentials of the sampling sites were valued.

The plant samples were propagated and tested for heavy metal tolerance according to the rooting test of WILKINS (1978).

The species have different sensitivity to the four metals. Both species are relatively insensitive to **lead** and **cadmium**, *C. epigejos* being more tolerant than *A. repens*.

A. repens is less sensitive to **zinc** than *C. epigejos*, but both species tolerate only very low test concentrations.

Compared with *A. repens*, *C. epigejos* is less sensitive to **copper**. The *C. epigejos* population from the copper smelter Legnica is tolerant to copper.

The results demonstrate that levels of sensitivity and of tolerance vary between species. Only in the species *C. epigejos* differentiation of tolerance levels between populations turned out.

D. A. WILKINS (1978): The measurement of tolerance to edaphic factors by means of root growth. THE NEW PHYTOLOGIST **80**, 623-633.

DYNAMICS OF ADAPTATION AND DIVERSIFICATION:
A 10,000-GENERATION EXPERIMENT WITH BACTERIA

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We followed evolutionary change in twelve populations of *Escherichia coli* propagated for 10,000 generations in identical environments. Both morphology (cell size) and fitness (measured in competition with the ancestor) evolved rapidly for the first 2,000 generations or so after the populations were introduced into the experimental environment, but both were nearly static for the last 5,000 generations. Although evolving in identical environments, the replicate populations diverged significantly from one another in both morphology and mean fitness. The divergence in mean fitness was sustained and implies that the populations approached different fitness peaks of unequal height in the adaptive landscape. Although the experimental time scale and environment were microevolutionary in scope, we observed several hallmarks of macroevolutionary dynamics, including periods of rapid evolution and stasis, altered functional relationships between traits, and concordance of anagenetic and cladogenetic trends. Our results support a Wrightian interpretation, in which chance events (mutation and drift) play an important role in adaptive evolution, as do the complex genetic interactions that underlie the structure of organisms.

Evolution of Baltic Sea *Enteromorpha* (Chlorophyta) based on nuclear rDNA ITS sequences

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The region from the ribosomal DNA (rDNA) including the 3' end of 18S rRNA, 5.8S rRNA, the 5' end of 28S rRNA and the internal transcribed spacers ITS 1 and ITS 2 were sequenced from four *Enteromorpha* species from the Baltic Sea. Two morphologically close species, *E. compressa* (L.) Greville and *E. intestinalis* (L.) Link., differed by only two nucleotide substitutions, and the coincidence of this difference with the morphological variation agrees with the concept of two separate species. *E. ahlnneriana* Bliding and *E. flexuosa* (Wulfen ex Roth) J. Agardh form another pair which is both morphologically and genetically quite distinct. The *Enteromorpha* sequences differ from those of other green algae in that the G+C content is very high in the ITS regions (up to 70%) even though that of the 5.8S rRNA is close to 50%. The conservative sequence of 5.8S rRNA is also used to examine the phylogeny of green algae.

Cryptobiosis, the Red Queen, and the myth of the ancient asexual

Ancient asexual lineages challenge the notion that sexual reproduction is maintained through co-evolution of hosts and their biological enemies. Efforts to account for the persistence of some asexual groups have focused on the potential effectiveness of cryptobiosis in facilitating escape from parasites. We show that, although cryptobiosis is common in asexual freshwater organisms, there is little evidence for the general antiquity of such taxa. As well, we note that the bdelloid rotifers, an apparently ancient asexual order, are attacked by a broad array of specialized parasites and predators. Collectively these observations suggest that cryptobiosis neither extends the evolutionary lifespan of asexual lineages, nor guarantees escape from parasites.

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I 1

THROUGH THE LOOKING GLASS: PARASITES, SEX AND CLONAL DIVERSITY
IN A NEW ZEALAND SNAIL

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Most eukaryotic organisms reproduce by cross fertilization, at least during some part of their life cycle. That this is true in spite of the costs incurred by biparental reproduction indicates that there is some very general advantage associated with meiosis and genetic exchange. Conversely, it would seem that there must be some severe disadvantages associated with the various kinds of uniparental reproduction, like parthenogenesis and self fertilization. The principal goal of this talk is to flesh out some recent empirical results on parasite-mediated selection for cross fertilization in a freshwater New Zealand snail (Potamopyrgus antipodarum). In the last few years, we have found that parasites are correlated with the frequency of sexual females among populations. These parasites (digenetic trematodes) castrate the snails, and thus impose strong selection for mechanisms that reduce the risk of infection. We have also found that many populations contain mixtures of sexual and parthenogenetic females, and that clonal diversity in these populations is very high (more than 100 different clones). Finally, we have found that there is heterogeneity in the prevalence of infection among clones within lakes, and the pattern of these differences is consistent with the idea that parasites are driving time-lagged, frequency-dependent oscillations of different clonal genotypes (i.e., the Red Queen hypothesis).

Discordance in population structure as revealed by different techniques.

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ITK

by

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Spatial and temporal genetic variation revealed by different techniques may yield different conclusions on the pattern of genetic variation and consequently on population structure. Data on temporal variation in brown trout (Salmo trutta L.) and on temporal and spatial variation in the sheep headfly (Hydrotaea irritans) are presented and possible causes of the discordance of different data types are discussed. When comparing temporal variation in mtDNA haplotype frequencies with nuclear allele frequencies in brown trout variation over time was found in haplotype frequencies but not in nuclear frequencies. This difference is explained by different effective population sizes on the two levels of up to 1/8 with a skewed sex ratio. In the sheep headfly significant differences in karyotype frequencies were found along a gradient from pasture to the center of the forest while allozyme frequencies did not reveal any differences between sampling locations.

Does reduced selection pressure on *Tribolium confusum* in a favourable environment decrease their fitness in this environment?

200

T11

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Some populations of plant and animals, e.g. those protected by a conservation programme or contemporary human populations in developed countries, have lived for several generations in favourable environments with a greatly reduced selection pressure. To test whether such reduced selection may diminish their fitness, populations of *Tribolium confusum* have been maintained for 17 generations in either favourable or harsh environments. In the favourable environment with an excess of food, mortality was low (3%). The contribution of individuals to the next generation was irrespective of their fecundity. In the harsh environment, the amount of food was severely limited and mortality exceeded 80%. Only those individuals which pupated first contributed to the next generation, and this contribution was proportional to their fecundity. Two populations were kept in the favourable environment and two populations in the harsh environment. In almost all generations test groups were drawn from each replicate to check their performance in the alternative environment, for either one or two generations. Such a design allowed comparison of both populations in both environments.

As expected, populations kept continuously in the harsh environment became adapted to it and showed considerably higher fitness than those kept in the favourable one. However, it does not prove that there was a general decrease of fitness due to reduction of selection pressure in the favourable environment. If such a decrease of their fitness occurred, the fitness of beetles from the favourable environment should be lower than those from the harsh environment, in the favourable environment too. After 17 generations, tests carried out in the favourable environment showed no statistically significant differences in fitness between populations from these two environments. Therefore, one may conclude that strongly reduced selection pressure for 17 generations neither decreases nor increases ability to survive and reproduce of *Tribolium confusum* beetles.

Phenotypic plasticity in fitness and morphological traits of the black bean aphid *Aphis fabae* reared on different host plants

201.

T11

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Phenotypically plastic responses in phytophagous insects can potentially facilitate the colonisation of new hosts. Consequently plasticity can reinforce differences in the ecological context promoting host race formation. We report the plasticity of the response of the black bean aphid (*Aphis fabae*) to two of its secondary hosts: broad bean (*Vicia faba*) and nasturtium (*Tropaeolum majus*). Measurements on morphological characteristics, a fitness index (r_m) and developmental rate (RGR) were made in clones obtained from different locations. There is significant genotypic variation in fitness and morphological characters over both hosts. Fluctuating asymmetries are highly correlated with fitness values. The results support the hypothesis of rapidly acclimation to a novel environment after continued exposure, with improving changes in the performance through the generations. The implications of the relationship between fitness, morphological characters and levels of fluctuating asymmetries in both hosts are discussed in the context of host race formation and speciation.

* Scholarship supported by CNPq, Brazil

— Is standing variation in quantitative traits due to allelic variants at 174
202 candidate neurogenic loci? Evidence from QTL mapping and quantitative
complementation testing in *Drosophila*

The implications of the molecular biology revolution have been great, yet at present very little is known about the molecular genetic basis of standing variation in quantitative traits. Experiments will be described which have the objective of identifying the nature of underlying genetic variation affecting a model character (bristle number) in a model organism (*Drosophila melanogaster*). Previous work by our group has used a QTL mapping approach to identify a few factors of large effect which account for much of the difference between lines artificially selected for increased and decreased abdominal bristle number. Mapped factors show sex specific effects, epistatic interactions, and have map positions corresponding to the position of candidate genes. Candidate genes are genes involved in bristle formation or patterning that have been identified through laboratory mutations of large effect. In order to determine if mapped factors are allelic to mutations at candidate genes we have conducted a series of Quantitative Complementation Tests.

Quantitative Complementation Testing is a novel genetic crossing scheme analogous to traditional complementation testing, but modified for quantitative traits. Results will be presented which provide evidence that mapped factors are either allelic to candidate genes or at least acting in the same pathway (i.e., dominant modifiers of the mutant). Candidate genes that show strong evidence of allelism now include: *extramachrochaetae*, *hairy*, *Delta*, and *bobbed*. With the exception of *bobbed*, these are all genes involved in the development of the *Drosophila* peripheral nervous system. The allelism of mapped factors to well characterized candidate genes will aid in the eventual identification of the molecular allelic differences which give rise to continuous variation, and ultimately allow estimation of the joint distribution of the frequency and allelic effects that are responsible for standing variation in these characters.

Long AO, Mullaney SL, Reid LA, Langley CH & Mackay TFC

IT

Molecular characterization of random amplified polymorphic DNAs (RAPDs) in *Pinus sylvestris*

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RAPD markers have been widely used in population and diagnostic studies of various plants. The molecular and genetic nature of the RAPD products, however, is not clearly documented. To characterize the molecular nature of RAPDs in *Pinus sylvestris*, we reamplified the segregating and non-segregating RAPD fragments and used them as probes in Southern hybridization to the RAPD profiles and total DNA digests of *P. sylvestris* individuals from different populations. The results showed that individual RAPD fragments resolved in the agarose gel often contain more than one DNA sequences, though with one sequence in predominant quantity. The additional co-migrating fragments, however, were few and did not affect the scoring of the RAPD bands. In some cases, Southern hybridization detected additional, but weak fragments in the RAPD profile that could not be detected by visual inspection of the corresponding agarose gels. The presence/absence polymorphisms revealed in the RAPD profile were confirmed by probing the RAPD filters with the reamplified polymorphic RAPD fragments. In contrast to other studies, RAPD fragments from *P. sylvestris* did not appear to originate from repeated sequences. Southern hybridization of total DNA digests to the reamplified RAPD fragments failed to detect variation among *P. sylvestris* individuals, even when polymorphic RAPD fragments were used as probes.

Keywords: *Pinus sylvestris*, RAPD, Southern analysis, genetic marker

single-copy sequences homology among the GC-richest isochores of the genomes from cold-blooded vertebrates

P2

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Vertebrate genomes are mosaics of isochores, namely of long, compositionally homogeneous DNA segments that can be subdivided into a small number of families characterised by different GC levels ^{1,2}. In the human genome, which is by far the most extensively studied, the compositional range of isochores is 30-60% GC. Five families of isochores have been identified in this genome: two GC-poor families, L1 and L2, representing together 62% of the genome, and three GC-rich families, H1, H2 and H3, representing 22%, 9% and 3-5% of the genome, respectively (the remaining DNA is formed by satellite and ribosomal NAS). A striking feature of the human genome is that gene concentration is extremely non-uniform and parallels GC levels. Gene concentration is low and constant over GC-poor isochores families L1 and L2, it increases over GC-rich isochores and reaches the highest level, more than 20 times that of the GC-poor isochores, in the richest isochore family H3.

We have hybridised the human H3 isochores on compositionally fractions of NAS from 3 fishes (*Tilapia butticoferi*, *Arotrhon meleagris* and *Oncorhynchus* etc) 2 reptiles (turtle and crocodile) and one amphibian (*Xenopus laevis*) species. Under conditions in which repetitive sequences are competed out, the H3 isochore probe only or predominantly hybridised on the GC-richest fractions of main-band DNA from all species investigated. These results indicate (as previously demonstrated for Birds and Mammals³) that single-copy sequences (which comprise coding sequences) from the human H3 isochore share homology with sequences located in the compositionally corresponding (GC-richest) compartments of the genomes tested. These results suggest that gene distribution is similar in all vertebrates genomes.

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Fig wasps, nematodes and the generation time effect in molecular evolution

The natural and evolutionary history of closely related species of fig pollinating wasps (Agaonidae), their parasitic nematodes (Parasitodiplogaster) and fig parasitic wasps (Agaonidae) associated with the same species of neotropical *Ficus* trees, provide a unique opportunity to test the effect generation time has on the rate of molecular evolution. Nucleotide sequences from two mitochondrial genes (COI and COII) were collected for a group of 10 species of fig pollinating wasps, their nematodes (only COII), and parasitic wasps collected from figs growing in the vicinities of the Panama Canal. Phylogenies were estimated providing evidence for cospeciation and allowing the comparison of the relative rates of molecular evolution in each of the three groups.

206 Sexual strategy of the trematode *Proctoeces maculatus* Odhner, 1911
in support of their population structure

T14

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At the marine ecosystems parasites form the ecological parasite-centric associations - Parasite Systems (PS) (V. N. Becklemishev, 1956). PS include the parasite population and host populations.

One of the complicated multi-component PS form the trematode *Proctoeces maculatus* Odhner, 1911 (*Fellodistomidae*) (*P.m.*). This species is very interesting because of the ecological plastics. Its environmental conditions diapason is very large, from Australia to Great Britain and from freshwater Black Sea to Red Sea with highest salinity. *P.m.* is a parasite of the different hydrobionts. Two years PS of *P.m.* was investigated at West Coast of Black Sea. It was revealed the *P.m.* population consist of three hemipopulation (HP). One is a parthenita, two are a hermaphrodite. It change the quantity, composition and sexual strategy during the year. The behavior of definitive and additional hosts is reason of this. The parthenita HP consists of numerous sporocyst microhemipopulations (MHP) and localized at coastal zone in mussel settlements. Its sexual strategy directs on reproduction of the MHP at cold seasons. The more variability components of PS are the hermaphrodite HP. That's why at the warm seasons parthenita HP has another structure and sexual strategy. This time it produces and exports the settle hermaphrodite larvae. The marita HP parasitized in fish populations doing the catadromal migrations. It is at coastal zone at the warm seasons only. This period of the population structure and sexual strategy of hermaphrodites direct on production and emission parthenita larvae - multiplication the number of MHP at mussel settlements. During cold seasons marita HP leave the coastal zone with fishes and reduce there. Parthenita HP is the basis of *P.m.* population.

How did forest trees colonize Europe ?

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Populations of forest trees exhibit a high level of genetic variation and a low level of differentiation even over very large distances (i.e. North America or Europe). This puzzling ability to preserve their biodiversity has been interpreted either as an effect of constant selective pressures or as the result of a significant amount of long distance dispersal. We want to show that these explanations meet serious difficulties when faced with the structuration of forest trees. Our hypothesis could lie in two peculiarities that share all forest trees: (i) they are long lived so that, in terms of number of generations, populations are relatively young (sometimes less than 100 generations since last glaciation) and consequently their conquest of temperate territories is a recent event (ii) they have a long lasting juvenile stage so that colonisation of new sites (after last glaciation) have been realised by numerous migrants and not by the progeny of the first ones. Tree populations thus reflect a "recent" colonisation process without any noticeable founder effect.

RFLP of a mitochondrial DNA fragment in several populations of Spanish brown trout (*Salmo trutta* L.).

Machordom, Annie; Zardoya, Rafael; Almodóvar, Ana & Bautista, José Manuel.

Spanish rivers have been stocked with hatchery populations of brown trout derived from specimens imported from central Europe.

With the aim of distinguishing between foreign and autochthonous brown trout populations, we analyzed by RFLP an amplified fragment of 3000 base pairs of the mtDNA.

Sequences of different nuclear or mitochondrial DNA genes did not show clearcut differences between natural and introduced trouts. However, this approach allowed discrimination between foreign specimens, and population polymorphisms as well.

Seven different compound haplotypes were found in the 13 localities sampled (7 rivers for natural populations and one sample of hatchery origin). Three of these haplotypes concentrated the 79.1% of the autochthonous individuals.

Both Duero and Tajo basins presented a particular haplotype each, with a frequency of 29.73% for the Tajo basin and 56.67% for the Duero basin.

This technique provided us with a rapid and not injurious method to identify the natural genetic diversity. This is essential to undertake adequate conservation and fish management decisions.

The Genetic Basis of Quantitative Variation: Candidate Genes and *Drosophila* Bristle Number
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The genetic basis of quantitative variation within populations and phenotypic divergence between populations and species is unresolved. Efforts to map the loci underlying phenotypic differences between strains have succeeded in localizing them to large genomic fragments that could potentially contain many loci affecting the trait. However, a considerable fraction of genetic variation for quantitative traits might be caused by wild type isoalleles at candidate loci identified from knowledge of the developmental and biochemical pathways determining the trait. If so, studying naturally occurring variation at these candidate loci enables us to understand the genetic basis of quantitative variation in terms of allele frequencies, effects and interactions, and ultimately to determine the molecular basis of phenotypic variation.

The relevant candidate loci for variation in numbers of sensory bristles in *Drosophila* are those involved in sensory organ development. Approximately 50 naturally occurring alleles of each of five of these loci - *Notch*, *scabrous*, *extramacrochaetae*, *hairy* and *Delta* - have been introgressed by 10 generations of backcrossing into the same standard inbred background. Evidence that allelic variation at these candidate loci accounts for much of the total genetic variation in bristle number will be presented. Pairwise epistatic interactions between introgressed regions containing wild type alleles at bristle loci with known developmental genetic interactions will be described.

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Observations of variation in the mating success of individual males on leks have been critical in the assessment of the role of female in sexual selection.

A series of models will be presented to quantify the potential contributions to such variation from a variety of processes: the sex ratio, variation in male quality, male attendance times, the degree of female synchrony in arrival at leks, female aggregation and female copying.

If matings are random pairings, then the variance in male mating success $V(s)$ increases proportionately with the sex ratio. If females arrive at leks synchronously and mate immediately, then $V(s)$ increases subproportionately as the sex ratio rises. Variation in male quality and all the other processes above result in a super-proportionate increase in the variance in male mating success.

This approach facilitates comparisons among studies of the potential for sexual selection. Data from over 70 leks from 20 species indicates that all leks exhibit greater variance than that expected by chance, and that there is a tight relationship between sex ratio and $V(s)$. In studies where it was possible to partition the component of variance attributable to differences in male attendance times at leks, on average 60% of the variance remained unexplained and may be due to (for instance) female preference.

Many workers in the field have described the acquisition by few males of many of the available matings with the term "skewed", and some have employed measures of skewness in studies. This approach will be challenged, and reasons why the variance in male mating success should be the measure of choice presented.

Evolution of drug resistance in the malarial parasite.

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Resistance to anti-malarial drugs is a severe problem in the control of malaria. Single locus mutations seem to be the cause of resistance to several of the drugs, although multiple loci are probably involved for others. This study addressed two questions. First, what is the probability that a newly arisen single locus or multi-locus mutant will survive in the parasite population given the stochastic nature of transmission, and second, what is the rate of increase in frequency of the mutants under natural and artificial (drug) selection pressures? The complex life cycle of the parasite comprises an asexual haploid stage in the host's blood, and a sexual diploid stage in the mosquito vector. During the blood stage multi-locus mutants act in an epistatic way if subjected to multiple drug pressure e.g. the fitnesses of two locus haplotypes when subjected to two drugs will be $\{1, 0, 0, 0\}$ for the genotypes $\{AB, Ab, aB, ab\}$ where upper case letters denote the mutant allele. If no drug pressure is applied, then if the mutant allele has a relative fitness of $1-s$ and fitness acts in a multiplicative way, the corresponding fitnesses will be $\{(1-s)^2, 1-s, 1-s, 1\}$. Thus if $s > 0$ natural and drug selection act in opposing directions the fate of a mutant will depend on the proportion of the host population which are treated with drugs and the fitness of the mutant alleles. During the sexual stage in the mosquito, multi-locus mutants recombine with other genotypes from the blood of the same host thereby causing a decrease in their frequency. The amount of loss through recombination depends on both linkage distance between the loci (r) and the type and frequency of the other genotypes. Thus tight linkage and high levels of inbreeding (due to fewer mixed infections) assist the mutant to increase in frequency under drug selection pressure.

In order to quantify these effects, a deterministic model which combined these three forces of selection by drugs, natural selection and recombination in the framework of host-mosquito-host transmission was built. Using the theory of branching processes, the ultimate survival probability of one and two-locus drug resistance mutants was predicted for various values of T , s , r and levels of inbreeding. It was found that higher rates of drug treatment increased the probability of survival of the mutant, especially when treatment occurred in the early generations after the mutation arose. Survival probability was also increased by higher and less variable transmission rates, tight linkage, fewer loci under drug selection, low natural selection against the mutant alleles, and high initial frequencies of other mutant allele involved were already high. Similar effects were found on the rate of increase in population frequency of a mutant haplotype which had already reached a significant frequency (1%) in the population as predicted using Markov chain techniques. However, results suggest that if only 20% of the population were treated and there was a 10% loss of fitness for each mutant allele relative to the wild-type allele mutants involving 2 or more loci would decrease in frequency due to the greater force of natural selection than drug selection. It was concluded that drugs should be used in combination and at minimum rate in order to prevent the spread of multiple drug resistance.

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T12

**GERMLINE AND SOMATIC INSTABILITY IN THE MEDFLY
Ceratitis capitata (DIPTERA, TEPHRITIDAE)**

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The mediterranean fruit fly, *Ceratitis capitata* (Diptera, Tephritidae) is probably one of the major agricultural pests in the world. It originated in Africa and within the last hundred years has spread to a number of countries, including the Mediterranean basin, America and Australia. On the basis of its economic importance, it became a target for accumulating information on the genome organization of the species. This information is also relevant to planning large medfly control and eradication programs using genetic methods.

Recently a syndrome of abnormal genetic traits that resembles *Drosophila* hybrid dysgenesis has been observed in the medfly hybrids obtained from crosses of different origin. These abnormalities include gonadal sterility, chromosomal breakages at male meiosis and instabilities at *white eye* locus. They seem to be restricted to the germline and environmental factors, such as temperature may influence their manifestation.

Genetic instability has also been observed at the *white eye* locus. This instability affected the germline and somatic tissues. Genetic data support the hypothesis that insertional mutations in the *white eye* locus cause the observed genetic instability.

The *white eye* locus of *C. capitata* is located on chromosome 5 where the most of the genes homologous to the X-linked genes of *Drosophila melanogaster* are located. In *Drosophila melanogaster* several unstable mutations on the X chromosome have the properties of insertional mutations.

GENETIC ANALYSIS AND PHYLOGENETIC INFERENCES AMONG SPECIES OF TEPHRITID FLIES.

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Multilocus enzyme electrophoresis data from 24 orthologous loci (212 alleles) were used to infer the genetic similarities between eleven Tephritidae pest species from *Ceratitis*, *Trirhithrum*, *Capparimyia*, *Bactrocera*, *Anastrepha*, *Rhagoletis*. For some of the considered species a different degree of genetic variability was evidenced which appears to be related to zoogeography and to the biological traits which are peculiar of each species. Nei and Cavalli-Sforza and Edwards genetic distances were used to express the genetic divergence and to infer phylogenetic relationships among the species. UPGMA clustering algorithm and the optimality criteria of Fitch and Margoliash, with (Kitsch) and without (Fitch) the tree constrained to have contemporary tips, were used. All the methods indicate the same clusters of species. One cluster is composed of *Ceratitis capitata*, *Trirhithrum coffeae* and *Capparimyia savastanoi*. Another is composed of *Rhagoletis cerasi*, *Bactrocera dorsalis* and *Bactrocera oleae*. A further loose cluster is comprised of *Ceratitis rosa* and *Anastrepha* species. The congruence between electrophoretic phylogeny and conventional classification is discussed. Our analysis also elucidated cases, within *Ceratitis* and *Bactrocera*, of interest from the evolutionary point of view, where allozyme dendrograms do not correlate well to morphological taxonomic relationships.

The population diversity of *Phytophthora infestans* in Russia revealed by PCR-based mtDNA analysis

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P16.

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A new PCR-based mtDNA RFLP analysis developed by Drs. G.W.Griffith & D.S.Shaw (pers. comm.) was used to study the population diversity of the heterotrophic oomycete *Phytophthora infestans* (Mont.) de Bary in Moscow region, Siberia (Tomsk), the Caucasus (Adler), and Belarus (Minsk). 84 isolates were collected from 1991 to 1994 from potatoes and tomato. Three mtDNA forms (Ia, Ib, and IIa denoted by Carter et al., 1990) were found by RFLPs of amplification products digested with restriction endonuclease MspI. The Ia form occurred in 20 (=71,5%) tomato and in 4 (=7%) potato isolates, the Ib - in 7 (=25%) tomato and 2 (=4%) potato isolates, and the IIa - in 1 (=3,5%) tomato and 49 (=89%) potato isolates. In conjunction with other markers (mating type and metalaxyl resistance characterized previously by Dr. A.Dolgova) 13 phenotypes were identified: 6 phenotypes among the 28 tomato isolates and 10 phenotypes among the 55 potato isolates. The Ib mtDNA form detected in both the potato and tomato isolates only with A1 mating type and metalaxyl sensitivity. The phenotype with A1 mating type, metalaxyl resistance, and the IIa form of mtDNA was present in 31 (=56%) of the isolates from potatoes and in only 1 (=3,5%) from tomato. In tomato isolates the most common phenotype with A1 mating type, metalaxyl sensitivity, and the Ia mtDNA was present in 17 (=61%) of the isolates, on the contrary, in only 1 (=2%) from potatoes. However, isolates representing the same phenotype were found as common in English sample in 1993 from potato (Dr. J.Day, pers. comm.). There was almost no genetic differentiation within Belarus and Siberian populations by contrast to the samples from Moscow region. Moscow potato population in 1993 was more polymorphic than in 1991. *P.infestans* population from the fruits have showed more little genetic variations than the population from the leaves. The population substructuring found among potato and tomato isolates probably confirms with a separate lineage of the populations from different host-plants due to specialization.

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Mimicry, raiation, and speciation in *Heliconius* butterflies
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The evolution of mimicry is a beautiful visual example of the origin of diversity. Simple Müllerian mimicry theory predicts that all unpalatable butterflies in an area will converge on identical colour patterns. In fact, mimicry rings have rampantly diversified, both sympatrically, between species of the genus *Heliconius*, and geographically, within and between species. In the 1970s, Christine Papageorgis suggested that Müllerian mimicry rings diverged under dual selection for mimicry and camouflage. I present data which casts doubt on this idea. The explanations for mimetic diversity more probably require warning colour divergence, race formation, speciation, microhabitat divergence and evolutionary inertia.

213 GENETIC VARIABILITY IN EUROPEAN NATURALISED STANDS OF
JUGLANS REGIA L. p5

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Abstract - Allozyme variation was examined in 41 accessions of *Juglans regia* L. The aim of this research was to assess the amount of variability of presumably still natural gene pool of *J. regia* in European countries where walnut is widely spread. The characteristic feature of allozyme variation found in this study was a high number of monomorphic loci. Only a percentage ranging from 45.9% to 50% of loci (P) was polymorphic (0.95 criterion). All accessions were characterised by a relatively high gene diversity (H_e), ranging from 0.178 to 0.243. Analysis of the apportionment of allozyme variation within and among accessions showed higher level of inter-population variability in accessions from Greece, Hungary, southern Italy and Sicily than in accessions from central and northern Italy and France. The patterns of allozyme differentiation for most Greek and Hungarian accessions corresponded to their geographic origin. In contrast, no such correspondence was found for Italian groups of accessions, except the Sicilian one which was relatively differentiated. Cluster analysis UPGMA, based on Nei's distances between all pairwise combinations of the 41 accessions, revealed two main groups: the first including most accessions from Hungary and Greece, the second, very heterogeneous cluster, comprising the remaining accessions from Italy and France, one accession from Greece and one from Hungary.

Divergent character of the two accessions from Greece (Crete and Macedonia) could be explained by their different origin. Historical trades between Crete and Italy could account for the observed similarity of this Greek accession to Italian ones. On the other hand, the Macedonia samples could represent a fragment of the natural *J. regia* distribution in Greece.

A reduced genetic variation within Hungarian accessions was found. Several biotic and abiotic factors could have contributed to the observed distinctiveness of the Hungarian accessions.

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GENOMIC INTERACTIONS AND SEGREGATION DISTORTION IN ARTIFICIAL HYBRIDS OF MOUSE

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The hybrid zone between *M. m. domesticus* and *M. m. musculus* in Europe shows a lack of sex chromosome introgression which indicates that some of their gene systems have differentiated sufficiently to cause disruption when they interact. The higher sensitivity of hybrid genotypes to parasite infestation also suggests a breakdown in the immune response. However, the differentiation of the two genomes does not always result in incompatibilities. There is less morphological bilateral symmetry in the parental populations on either side of the zone than in the hybrids from the centre which suggests that there is a greater developmental homeostasis in mice with hybrid genomes.

A genetic study of controlled crosses between the two subspecies was conducted to study the degree to which the two hybridizing taxa are functionally differentiated and to identify the loci or chromosomal regions involved.

So far 40 microsatellite markers spread out in the whole genome have been analysed in the backcross generation. We have detected preferential X chromosome associations supporting the hypothesis of coadapted gene systems. The proximal region of the X chromosome shows transmission ratio distortion in favour of the *musculus* type variant, suggesting either the existence of a distorter locus in that region or a locus under selection. This effect though, is limited to the females, probably due to stronger selection against the X-Y heterospecific combinations in males. The transmission pattern of some autosomal markers shows a strong deficit of heterozygotes in males suggesting that selection is stronger against the heterogametic sex. Segregation distortion is rarely detected for the autosomal markers and is always in favour of the *domesticus* alleles, which is compatible with the general direction of asymmetrical introgression found in the hybrid zone.

SYNERGISTIC SELECTION ON WARNING COLORATION: EXPERIMENTS WITH TRADITIONAL AND NOVEL SIGNAL

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In this study we tested the idea of synergistic selection (green beard effect) in evolution of warning coloration. Selection is synergistic when individuals share the same phenotype benefiting from their phenotypical similarity, not necessarily from their relatedness. We examined the reactions of wild caught great tits to novel unpalatable prey with 1) traditional signal (black and yellow) 2) novel signal (light pink) and 3) no signal (control) when prey were offered either in groups or solitarily.

Our results showed that reactions of birds toward unpalatable prey depended significantly on spatial distribution of prey (grouping vs. solitary) and the type of the signal. Birds avoided more the traditional black and yellow signals than novel pink signals. However, when pink prey items were offered in groups, birds seemed to show immediate reluctance to attack them. Thus, aggregation enhanced the function of the colour. Birds did not show, during their first encounter, any avoidance of pink preys when prey were offered solitarily but they did avoid black/yellow prey already in this situation. Our results demonstrated the importance of synergistic selection in the evolution of warning coloration. Unpalatable prey individuals benefit strongly by using similar colour patterns than others. Individuals with a new signal may, however, evolve through kin selection.

Reproductive costs and litter size in the bank vole

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Life history theory is based on the assumption that trade-offs exist between various life history traits of individuals. The present study is the first one to examine trade-offs in free-ranging mammals by manipulating litter size. We studied the consequences of nursing different numbers of offspring for both the offspring and for the mothers in the bank vole (*Clethrionomys glareolus*). In this territorial species the breeding success of females is supposedly constrained by competition for space. Here we were able to investigate whether the size of home range correlates with the initial litter size of females and how home range size will vary in response to litter size manipulation.

Results

Litter enlargement did not increase the number of weanlings per mother. The weight of juveniles was significantly lower in the enlarged litters and higher in the reduced litters compared to the control group. However, the survival of juveniles from weaning to the age of three months did not depend on their weight at weaning. Data from a previous study indicated that the higher weight at weaning may increase juveniles' abilities to mature and breed during their summer of birth. Manipulation of litter size did not affect significantly the weight or survival of mothers or the success of subsequent breeding. The size of home ranges correlated positively with the initial litter size. However, space use by females did not change with the degree of manipulation.

Discussion

Our results indicate that females nursing enlarged litters produce smaller offspring at weaning with no residual effects on future maternal survival or reproduction. Mothers did not seem to compensate the nursing costs with increased parental effort, which should be reflected in the condition of mothers or in the use of resources, e.g. in an enlarged size of home range. Probably, the possibility to gain a larger home range is constrained by other breeding females in a saturated breeding population. These results may support the individual optimization hypothesis, that a female produces that size of litter which gives the best present reproductive success in the environment where offspring are nursed.

MOLECULAR CHARACTERIZATION OF THE BaB300 SATELLITE DNA FAMILY IN BACILLUS STICK-INSECTS.

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Genomic DNAs of two bisexuals (Bacillus rossius, B. grandii) and of their hybrids have been tested for the presence of the highly repetitive satellite DNA family "BaB300", first found in the grandii-like parthenogen B. atticus (Mantovani et al., Ins. Mol. Biol. 2:141-147, 1993)

Multimeric ladders of the 300 bp monomer were obtained with 6 endonucleases (AluI, TaqI, BglII, ClaI, DraI and EcoRI) of the 20 tested from the genomic DNAs of B. grandii subspecies and of B. whitei (= rossius/grandii); taxon-specific differences in monomer amount were also scored. On the other hand, no BaB300 satDNA was found in genomic digests of B. rossius.

Southern blots with DIG-probes cloned from each species revealed cross-hybridization among B. atticus, B. grandii and B. whitei.

In situ hybridization showed a pericentromeric localization of the BaB300 family on all chromosomes of B. grandii, on the grandii haploset embodied in B. whitei and on a subset of chromosomes in B. atticus.

Sequence data support the existence of a unique satellite family in the atticus-grandii group and in their hybrids with B. rossius, sequence homology percentages ranging from 80 to 97%. Dendrograms obtained from sequence comparisons showed a species clustering pattern. It is to be noted, however, that within the all-female B. atticus clones derived from the same zymore or cytotype do not cluster together, but are randomly scattered and intermingled.

The very high level of BaB300 sequence homogeneity ascertained in B. atticus in spite of the occurrence of cytological-allozymatic differentiation and of its parthenogenetic reproduction could suggest the existence of molecular constraints on this satDNA, possibly related to its centromeric localization.

Molecular analyses support morphological, karyological and allozyme data on the existence of two well differentiated species-groups within the genus Bacillus, the atticus-grandii and the rossius artenkreis (Scali et al., Boll. Zool. 62:59-70, 1995), thus reinforcing the taxonomic value of the genomic approach.

Genetic structure and divergence of *Polyommatus coridon* (Lepidoptera: Lycaenidae) from the island of Sardinia.

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The *Polyommatus coridon* species complex is distributed throughout Europe. The taxonomy of the group, mainly based on wing pattern and coloration, is still debated. In recent years the presence of *P. coridon* has been ascertained in the islands of Corsica (Schurian, 1977) and Sardinia (Leigheb, 1987, 1991). In Sardinia *P. coridon* is represented by a small population restricted to a few localities in the central massif of Gennargentu. A subspecific status (*gennargentii*) for the Sardinian taxon has been proposed based on distinct morphological features of both males and females. Electrophoretic analysis of 17 enzyme loci was used to assess the genetic differentiation of the Sardinian *Polyommatus coridon* from *P. coridon* of peninsular Italy (ssp. *apenninus*) and the related taxon *P. caelestissimus* from central Spain. From the analysis of allozymic data the Sardinian *P. coridon* appears as an isolated, strongly inbred, population with very low level of genetic variation ($P=17.6\%$, $H=.024$) with respect to the continental populations ($P>50\%$, $H\geq 0.170$) from which probably it derived. Restriction in gene flow is sustained by the presence of alternative fixed alleles at the *Aat*, *Gpi* and *Pgm* loci and significant differences in allele frequencies at other loci discriminating the Sardinian population from the peninsular *P. coridon* and *P. caelestissimus*. Nei's genetic distances of *P. c. gennargentii* from *P. caelestissimus* ($D=.337$) and *P. c. apenninus* ($D=0.434$) suggest the evolution of the Sardinian taxon along an independent lineage, supporting a modification of its taxonomic status as originally proposed by Leigheb. On the other hand, substantial gene flow exist between the two continental taxa ($D= 0.054$). The lower *D* value between the Spanish and Sardinian taxa seems to support the hypothesis of a closer relationship with *P. caelestissimus* from which *gennargentii* was speculated to be derived based on morphological similarities after the split of the Sardinia-Corsica landmass from the Iberian peninsula (about 29 Myr). However, considering the wide distribution and relic characteristics of this species group, additional investigation will be necessary to clarify the phylogenetic relationship among the members of the *P. coridon* complex.

Reproductive decisions and life history tactics in Soay sheep

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Soay sheep on St Kilda show persistent instability, with population cycles culminating in high mortality every three or four years. Because Soay sheep are a primitive breed of domestic sheep, it is possible that they have in the past been selected for high fecundity and their fecundity is now maladaptively high for their environment, contributing to the population crashes that are observed. Births and mortality have been monitored in detail in this population since 1985, enabling estimates of the costs and benefits of reproductive decisions to Soay ewes to be made. We use estimates of the costs and benefits of different reproductive decisions (to produce one lamb or two, or to avoid breeding) to construct an optimisation model to predict the reproductive behaviour that ewes should perform. Since we are concerned with the optimisation of sequences of actions we use stochastic dynamic programming to predict optimal reproductive decisions. We compare the predictions of the model with observed behaviour to assess whether this behaviour is adaptive. Our results show that, contrary to expectation, the reproductive decisions that ewes make are close to optimal, given that they do not have information about the population cycle.

EVOLUTION OF THE *Pgd* REGION IN *Drosophila subobscura* RELATIONSHIP BETWEEN CHROMOSOMAL AND MOLECULAR POLIMORPHISM.

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The *Pgd* gene of *Drosophila melanogaster*, that encodes the enzyme 6 Phosphogluconate dehydrogenase (6PGD), is located close to the telomere of the X chromosome (X-2D) whereas in *D. subobscura* it is located at a more internal region (13A) of chromosome X (=X). Both allozyme (generally 6PGD¹⁰⁰ and 6PGD⁹²) and chromosomal polymorphisms (A₁, A₂, A₂₊₆, A₂₊₃₊₅₊₇,...., some of them showing clear latitudinal clines) are found in natural populations of this later species. It is well documented that one of the allozyme variants (6PGD⁹²) is in strong linkage disequilibrium with the chromosomal gene arrangement A₂.

A region of 7.8 kb including the *Pgd* gene has been cloned and sequenced in *D. subobscura*. Comparison of this 7.8 kb fragment with the homologous region of *D. melanogaster* reveals the presence of two flanking transcription units and the breakpoint of a fixed inversion. Levels of nucleotide divergence, both for synonymous sites (K_s) and for amino acid replacements (K_a), has been estimated for the three transcription units. In addition, nucleotide polymorphism, in relationship with variation at the chromosomal and allozyme levels (this latest only for the *Pgd* locus), has been analyzed in two natural populations of *D. subobscura* from different latitudes (Barcelona and Marraques).

EGG DESTRUCTION BEHAVIOUR BY GREAT SPOTTED CUCKOOS: ADAPTATION OR

EXAPTATION?

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Great spotted cuckoo females (Clamator glandarius) lay their eggs getting across the host's nest in a few seconds, and normally dropping them from the rim of the nest. This behaviour results in the damage of host's eggs, as a consequence of the thick shell of cuckoo eggs. In the magpie (Pica pica), eggs are usually crushed or cracked, and in a few cases pecked. In this study we analyse the frequency and type of egg destruction, and its possible role enhancing the breeding success of the cuckoos. As the great spotted cuckoo eggs have a shorter incubation period than magpie eggs, they usually hatch several days before magpie eggs, and magpie chicks starve in the competition for food with the larger cuckoo chick. However, there is a significant difference in breeding success between eggs laid early (during the magpie laying sequence) and eggs laid late (after clutch completion). In the last case, cuckoo hatching and fledgling success is lower. To understand the function of egg destruction we have compared cuckoo success in natural nests (naturally parasitized nests with broken host's eggs) with cuckoo success in experimentally parasitized nests (without egg destruction), simulating early and late laying.

Results show that egg destruction is adaptive only when cuckoo eggs were laid late. In this case, egg destruction improves hatching success and reduces the number of nestlings competing with the cuckoo chick. However, there are no differences in breeding success between control nests and experimental nests in which we simulated an early laying. The results point out that egg destruction should be carried out only when a parasite is laying late (in the only moment they get benefits) but it happens when they lay early as well. If egg destruction behaviour is considered an adaptive tactic, we should expect a higher proportion of host eggs destroyed when late laying, and different proportions in the type of breakage. In fact, the type of damage and the proportion of eggs damaged do not vary with the moment in which the cuckoo egg is laid.

Laying as quick as possible is an advantageous tactic when hosts are larger than parasites (as it is the case in the magpie-great spotted cuckoo system). Egg laying behaviour incidentally enhances offspring success by destroying host eggs, hence this behaviour could have been maintained as an exaptation rather than an adaptation.

Population Cytogenetics of a Hybrid Zone in *Chorthippus parallelus*: a Review

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The two grasshopper subspecies *Chorthippus parallelus parallelus* and *C. parallelus erythropus* are respectively distributed throughout northern and eastern Europe, and in the Iberian peninsula. A series of contact zones are formed where the subspecies ranges meet in the Pyrenees. We review recent population cytogenetic studies of pure and hybrid populations.

Most of the chromosomal variation associated with differentiation of the subspecies occurs in the sex chromosomes: the presence or absence of two C-bands, and an active NOR. A third C-band has been found whose distribution appears to be confined exclusively to individuals from populations of one contact zone. These characters exhibit distinct patterns of clinal variation, consistent with explanations of different modes of maintenance: neutral, introgressive and adaptive.

Further study of the inheritance of C-bands, and patterns of fertilization, fecundity and viability in a hybrid population reveals differences between C-band karyomorphs that may be associated with differential fitness of pre-diapause embryos in field populations.

We discuss the relevance of these studies to current aspects of interest in evolution in hybrid zones and of biogeographic variation.

The effect of pollen limitation on plant reproductive systems 222 and the maintenance of sexual polymorphisms

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Sandrine Maurice

Abstract

Insufficient pollination can affect the reproductive output and the rate of outcrossing of individual plants. We use a phenotypic model to explore the effect of pollen limitation on the evolution of plant reproductive systems. Compared to situations without pollen limitation, we show that conditions for the stability of different reproductive systems can change under pollen limitation: hermaphrodites are maintained under a larger set of conditions at the expense of unisexual types, especially males. We also show that trioecy, i.e., coexistence of hermaphrodites, males and females, can be evolutionarily stable, which is not the case in the absence of pollen limitation.

Phylogenetic Relationships Among Families of Modern Frogs (Bufonoidea): Insights from Mitochondrial Gene Sequences. I. Ruvinsky*, and L. R. Maxson*. *Department of Biology and Institute of Molecular Evolutionary Genetics, Penn State University, University Park, PA 16803, USA.

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Nucleotide sequences of portions of the mitochondrial 12S and 16S ribosomal RNA genes were used to further evaluate phylogenetic relationships within the anuran suborder Neobatrachia. An analysis of nine hundred nucleotides from each of eight new representatives of the Dendrobatidae, Hylidae, Leptodactylidae and Myobatrachidae plus all other available members of the Neobatrachia confirms the monophyly of this anuran suborder. There is also strong support for two major monophyletic lineages (Bufonoidea and Ranoidea) within the Neobatrachia. The Neotropical Bufonoidea and their derivatives are clearly distinct from the Old World taxa. The latter show an interesting association of the two Australian Myobatrachids with the African Heleophrynidae, while the Sooglossidae remains the most basal Bufonoid lineage. Within the New World stock, the monophyly of the Dendrobatidae was strongly supported and an Australian hylid (Pelodyadinae) shows close affinity with the South American Phyllomedusinae. A group comprised of Hylinae, Centrolenidae, Bufonidae, and Hemiphractinae, with the latter two clustered, was significantly supported. The addition of new taxa has allowed us to define some of the relationships within the suborder Neobatrachia and provide suggestive evidence that some well established families (Hylidae, Leptodactylidae and Myobatrachidae) may not be monophyletic.

Animal Language and Human Language

John Maynard Smith

A major problem in animal communication is the evolution of reliability. Crudely, what keeps signals honest? Various evolutionary processes that can ensure reliability will be discussed.

In humans, linguistic competence is peculiar, both in the sense of being peculiar to humans, and of being special to language and not merely an aspect of general intelligence. The evolutionary origins of linguistic competence will be discussed, and evidence for genetically determined variation in competence will be described.

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**Direct and correlated responses to selection on wing
area with constant cell size in *Drosophila melanogaster***

Temperature has been strongly implicated as a selective variable influencing body size in *Drosophila melanogaster*. Both laboratory experiments and studies of geographic clines have shown that evolution in cool conditions leads to an increase in adult body size. The difference in body size between cultures kept in the laboratory for many generations at different temperatures is achieved by a change in cell size, rather than cell number. In contrast, the clinal geographic variation in body size is mainly caused by a change in cell number, with only a small effect on cell size.

To disentangle the effects of body size and cell size on thermal adaptation three replicates of each of three selection regimes (large, small and control) were set up. Wing area was selected to increase under the 'large' selection regime and to decrease under the 'small' regime, while average cell size was not allowed to change relative to the control lines. After 8 generations the selection lines had diverged, enabling direct examination of the consequence of altered body size, achieved through changes in cell number, for thermal adaptation by investigating the relative fitnesses of the selection lines at 18°C and 25°C.

225 Species richness on coral reefs across the tropical Indo-west Pacific (IWP) is extraordinary. Yet despite over a century of biogeographic work, the evolutionary mechanisms underlying the origins of high IWP diversity remain unclear. Examination of the pattern of mitochondrial DNA variation in "species-complexes" of IWP butterflyfish (Chaetodontidae) highlights a recent period of species formation within this region. For groups of morphologically identical species that differ in colour pattern, concordant phylogenetic patterns and slight genetic differences in a 495 base segment of the mitochondrial cytochrome b gene suggest that genetic differentiation was influenced by common environmental changes. Indeed, within the Pacific, cytb differences among species in three "complexes" suggest that differentiation occurred within the last 300-700,000 years. The pattern of mtDNA variation within the rapidly evolving mitochondrial control region for the three Pacific members of one of these "complexes" traces a period of significant demographic change over this period. From a common ancestor, mtDNA variation initially coalesced into three major lineages. This period of coalescence of mtDNA variation appears to have been followed by a period where mtDNA variation was buffered from extinction. This phylogenetic pattern is most consistent with a wave of demographic expansion from small effective population sizes. High dispersal due to a long lived planktonic larval stage and few reproductive barriers has resulted in the nearly random distribution of two of these lineages both across the Pacific and between species designations based on colour pattern. The third lineage shows much higher levels of geographic and species specificity. Phylogenetic and demographic patterns emerging from molecular and paleontological studies of IWP gastropods, crustaceans, and echinoderms paint a similar turbulent evolutionary picture of the IWP challenging previous notions that the extraordinary of this region diversity reflects long-term stable environmental and physical conditions.

225a The bluebottle *Calliphora vicina* (Meigen) (Diptera: Calliphoridae) is a carrion fly with a wide distribution across Europe. Larvae produced during the summer develop into flies without interruption but those produced later in the year overwinter as late third instar larvae. Larval diapause is induced by the photoperiod (daylengths) experienced by the maternal generation rather than by the onset of cold temperatures during larval growth. Day length is a reliable indicator of season as it varies predictably across the year and can be used as a cue to future changes in the environment. Diapausing larvae are more tolerant of cold than non-diapausing larvae. Diapause is terminated in spring by rising temperatures which induce pupation and metamorphosis to the imago.

I have maintained different geographic populations of *C. vicina* in the laboratory and investigated the photoperiodic conditions necessary to induce diapause. Differences between the populations' responses to different daylengths were revealed by keeping cages of flies at a variety of photoperiods ranging from constant darkness to constant light and rearing the larvae in the dark. The critical day length (the photoperiod at which 50% of larvae enter diapause) is longer in northern populations and the period to spontaneous recovery from diapause is also longer.

Such characters are probably under genetic control since they are retained by populations reared under constant laboratory conditions. These differences can be explained in terms of adaptation to the different selective pressures in the original habitat of the flies. Northern insects must be prepared to induce diapause in their offspring at daylengths when those of southern populations are still developing due to the earlier onset of hostile conditions at high latitudes. Flies with a long critical daylength are selected at high latitudes whilst those that continue to produce developing larvae at shorter daylengths are favoured further south.

The emerging relevance of evolutionary biology to applied problems and opportunities: a workshop report

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The goal of this workshop was to bring together selected experts with a variety of perspectives from diverse backgrounds and challenge them to identify roles that can be played by evolutionary biology in addressing applied problems and opportunities faced by society today. Key areas explored were **Phenotypic Expression in Novel Environments** (e.g. planned introductions of genetically engineered organisms; agro-ecosystem management), **Environmental Biotechnology or Bioremediation** (e.g. preadaptation of biodegradation processes in soil microorganisms; population dynamics in *in situ* treatment), **Novel Products and Processes** (e.g. natural products prospecting, bioprocessing), and **Biodiversity and Conservation** (e.g. genetic diversity, species diversity, habitat diversity). A small group of highly credible participants (approximately 45) were invited representing academic evolutionary biology, government and private agencies, and private sector companies. During the workshop, carefully designed sets of questions were tackled during facilitated break-out sessions. Responses have been captured in a workshop report, which will be disseminated to a variety of audiences, including evolutionary biologists, interested industry representatives, policy makers and funding agencies. The report identifies specific points of potential application of evolutionary biology to current socially relevant issues, points toward the field's role as new issues or trends emerge, outlines mechanisms or pathways through which evolutionary biology can actually make its contributions, and discusses policy implications for facilitation of research, education, and technology transfer. Crystallization of such recommendations by recognized leaders should help lead to an ongoing infusion of the insights of evolutionary biology into important issues confronting society today.

(key terms: flow cytometry/phenotypic evolution/repetitive DNA/*Silene latifolia*)

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Since its discovery, repetitive DNA has been regarded as evolutionary "junk" with little phenotypic impact. Phenotypic evolution has typically been studied using quantitative genetic techniques that treat underlying genetic effects as variance components. In previous work, we identified an among population negative correlation between nuclear DNA content variation, attributable to repetitive DNA, and calyx diameter, a phenotypic character, with obvious ecological importance, in *Silene latifolia*. In the present study, we established a negative genetic relationship between an AT-biased flow cytometric measure of nuclear DNA content and calyx diameter across lineages selected for increases or decreases in flower size. Our present results suggest that variation in repetitive DNA may underlie response to selection on phenotypic characters.

Genetic variability in different subspecies of *Parnassius
mnemosyne*

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Parnassius mnemosyne is a highly polytypic species. Over 70 of its described infraspecific taxa, which can be grouped into five big subspecies groups, of which three occur also in the Carpathian basin. The distribution of this species is strongly decreasing in Western and Central Europe often resulting in isolates which may become endangered. In Hungary, however, there are still fairly strong populations in addition to some small isolates.

Our aim was to explore the trends in genetic variability and genetic differentiation within and between subspecies.

Genetic variation was studied by means of horizontal gel electrophoresis at 12 loci.

Our results showed that the allele frequencies greatly differed among the populations even within a subspecies. The main evolutionary force acting on the populations is genetic drift and the populations are probably subdivided.

Cladistic analysis of combined datasets to resolve radiation events in Aeonium (Crassulaceae).

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The 41 species of Aeonium of the succulent plant family Crassulaceae constitute a well known example of adaptive radiation. Markedly different growthforms have evolved in the genus, ranging from small herbs, and large hapaxanth rosettes to rosette trees and tall, branched (sub)shrubs. Thirty eight species of Aeonium occur in Macaronesia, one in Morocco and two in East Africa and Arabia. Recent phylogenetic analysis indicates that Aeonium and the related Macaronesian genera Aichryson and Monanthes are monophyletic and that the Moroccan Sedum series Monanthoidea is the sistergroup of the Macaronesian genera. The East African, Arabian and Moroccan species of Aeonium have reached their current distribution through remigration to Africa.

Although our understanding of the evolution of the Macaronesian Sempervivoideae has substantially improved by molecular studies using both nuclear and chloroplast DNA, several parts of the phylogeny of Aeonium are still unresolved as a result of high speciation rates relative to the mutation rate of most DNA regions. The use of highly variable molecular data which would allow the resolution of periods of rapid speciation however, is often compromised by the age of a radiation. Therefore, adding characters more intimately associated with cladogenesis than molecular data is probably valuable.

Data from morphology, secondary compounds, the chloroplast genome (intergenic spacer sequences, RFLPs), and the nuclear genome (ITS2 sequences, RAPDs) were combined and cladistically analysed. After analysis of each dataset separately, datamatrices were combined rather than trees. Cladistic analysis of the combined datasets resulted in increased levels of resolution, stronger support for clades, and lower levels of homoplasy and improved interpretation of the modes of speciation, biogeographical patterns and the evolution of growthforms in Aeonium.

Adaptive Dynamics and Evolutionarily Singular Strategies geometrical consequences of nearly faithful reproduction

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I shall present a simple representation of the adaptive dynamics of phenotypic traits. The basic assumptions are that (i) reproduction is clonal or inheritance haploid, (ii) evolution is essentially mutation limited, (iii) there exist sufficiently smooth functions $s(Y)$, $s_X(Y)$, $s_{X_1X_2}(Y)$, etc., such that the sign of $s(Y)$, $s_X(Y)$, $s_{X_1X_2}(Y)$, ... , tells us whether a Y clone can invade into the virgin environment, a monomorphically X population, a combination of an X_1 and an X_2 population, etc., and (iv) mutations have only fairly small effect, although each of these assumptions except (iii) may be relaxed. Within this context I shall analyze, for the case of a one dimensional trait space, the generic types of dynamically singular trait values. This approach *i.a.* clarifies in which sense the usual conditions for evolutionary stability (or rather Evolutionary Unbeatability!) are but a part of the conditions for dynamic stability. The resulting geometrical classification can *i.a.* be used for developing a bifurcation theory of Evolutionarily Stable Strategies and coalitions of finite numbers of such strategies, independent of the details of the original dynamic context.

CHROMOSOME EVOLUTION IN GENUS *GLYPTOTENDIPES* Kieffer
(DIPTERA, CHIRONOMIDAE)

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In the present paper the role of polytene chromosomes in the systematics and speciation of the genus *Glyptotendipes* is discussed. The sibling species: *G. barbipes* and *G. salinus* are distinguished by homozygous inversions, as well as by quantity and quality of centromere heterochromatin of 1st, IIrd and IIIrd chromosomes of both species and by the position of the nucleolus of the IIIrd chromosome. The DNA content in the centromeres of *G. barbipes* is double that of *G. salinus*. It could be possible that these species share a common library of satellite sequences which were amplified to various degrees so that in every species one may see different amounts of DNA. Comparison of chromosomes on one hand and crossing experiments on the other led to the conclusion that *G. barbipes* and *G. salinus* are closely related. On the basis of the differences it is assumed that the karyotype of *G. barbipes* is more recent evolutionary product.

The data from karyological analysis of *G. gripekoveni* and *G. glaucus* showed that genetical non homogenous groups (cytotypes) of these species had been formed in an investigated material (Bulgarian, Hungarian and Spain populations). A new species, with $2n = 6$, with a new chromosome arm combination: AB, CD, GEF is found in a Spain population. The formation of species with a reduced chromosome set is discussed. An introgressive hybridization between different cytotypes of both species is established. The detailed comparative analysis with a type material shows that the two cytotypes of *G. glaucus* belong to two different species: *G. glaucus* and *G. pallens*. A hybrid has been produced between these species. The both species are distinguished by homozygous inversions, band sequences of IVth chromosome, the appearance of the heterochromatin, as well as by an external morphology.

Further analysis with particular attention to the micro-ecology, may shed light on whether larvae of other cytotypes have different ecological requirements, and in particular whether these cytotypes belong to different species.

Effects of pollution on the polytene chromosomes of Chironomus riparius Meigen 1804 (Chironomidae, Diptera) from a river Po station.

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Chironomus riparius ($2n = 8$ with chromosome arm combination AB, CD, EF, G, a nuclear organizer and 3 Balbiani rings in the 4th chromosome) has a well done standard chromosomal map. A population of this species from river Po near Moncalieri (a very heavy metal polluted station) was studied for two subsequent generations.

Individuals of this population show their genome mobilized by means of different chromosome rearrangements, such as para-heterozygous inversions, deletions and deficiencies and changes in functional activity and appearance of heterochromatin.

In arms A, B, C, D, E, F we observed an increased size of some bands, in contrast with the standard chromosomal map. A same band could appear in heterozygous or normal homozygous state or as an amplified band. In arms A and F we established two unknown puffs. Disturbance in pairing of arms E and G as well as heterozygous Balbiani rings and NORs were observed. Very often the 4th chromosome was very heteropycnotic and looked like a "pompon" chromosome.

For the first time in this species, a high frequency of ectopic pairings of different arms was observed. Telomeric regions involved in ectopic pairings changed their structure and appeared granulated. Occasionally, in centromeres of all chromosomes the same heterochromatic change was observed. It could be due to some external agents having some inhibiting effect on proteins which participate in chromatin condensation.

The hypothesis is advanced that such high frequency of different structural rearrangements could be correlated with distribution of specific mobile elements, called "Cla- elements".

Probably stressful environmental conditions influenced DNA under-replication during the development of salivary gland chromosomes, but mechanisms could be present in this species that enable cells to face adverse environmental conditions.

Sperm exchange in the planarian flatworm Dugesia polychroa, a simultaneous hermaphrodite: do they trade sperm ?

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Simultaneous hermaphrodites are expected to mate primarily to donate sperm (paternal RS) rather than to receive sperm (assuming that the female function is rarely sperm depleted and that matings only offer genetical benefits). Starting from the *reverse* assumption that they should *avoid* donating sperm, Leonard and Lukowiak (Am. Nat. 1984) predicted that hermaphrodites should show reciprocal and parcelled sperm exchange or "sperm trading". It is true that many hermaphroditic taxa have reciprocal insemination preceded by elaborate pre- and in-copula courtship behaviour. But is this conditional sperm trading or is it a direct consequence of the identical interest of both partners to inseminate each other? We tested an alternative model for the evolution of sperm trading (Michiels & Weinzierl, unpubl.). It states that, in hermaphrodites promiscuous, frequent mating is expected. This leads to sperm competition and increased investment in sperm, resulting in the evolution of sperm digestion in the receiver. If matings are frequent and not costly, such situation promotes the evolution of conditional sperm trading.

We investigated the copulatory behaviour of the freshwater planarian flatworm Dugesia polychroa and looked for support of our model using behavioural observations, mate choice experiments and histological techniques in the lab and on animals collected in the field.

Although fertile sperm are stored for > 3 months in isolated individuals (selfing does not occur), mating is frequent in the lab (1 mating every 1.7 day) as well as in the field (estimated: once a week). Pre-copulatory courting is absent. Copulations are random with respect to size (a strong indicator of maternal quality). Copulation duration ranges from 5-150 min (avg. 60 min) and is clearly bimodally distributed. "Short" copulations (< 35 min, 30% of all copulations) are without sperm transfer, whereas "long" copulations (≥ 35 min) always involve sperm transfer, usually reciprocal. Male allocation is high in comparison to other hermaphrodites. The amount of sperm available in the sperm ducts allows for about 4 matings in brief succession. Sperm are transferred in clumps that vary little in size, but large animals tend to produce larger clumps. In the bursa copulatrix (sperm receiving organ in the tail-end) sperm clumps are digested within 3-4 days. Sperm migrate to the sperm receptacles (sperm storage organs behind the head) within 15 hours. A large proportion of them are digested by yolk funnel cells along the oviducts.

The data suggest that D. polychroa is a promiscuous, multiple-mating species with adaptations to high levels of sperm competition such as high male investment and digestion of allosperm. Frequent, short copulations without sperm transfer tentatively suggest the existence of an *in-copula* mechanism to control or estimate the likelihood of reciprocal sperm exchange.

Pollen aperture morphogenesis : what is the range of possible forms ?

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Pollen grains of flowering plants possess, in most cases, apertures that are thinner areas of the pollen wall. Physiologically apertures are germination zones or a harmomegathus (device to accommodate volume changes) or both. Angiosperm pollen grains display a wide variety of aperture arrangements, of which the two most widespread involve either a single distal aperture or three radially symmetrical equatorial apertures. The former arrangement predominates in monocotyledons and magnoliid Dicotyledons and the latter in "higher" Dicotyledons or Eudicots. Other arrangements derived from the basic patterns occur in both monocotyledons and Dicotyledons.

Considering only species which belong to the three-aperturate pattern, some of them are able to produce pollen grains with different aperture numbers within the same anther. This phenomenon, we called pollen aperture heteromorphism, is relatively frequent (33% of the 186 sampled species; Mignot et al., 1994). The occurrence of several pollen types within the same anther raises the question of their morphogenesis. We have then observed different stages of the pollen morphogenesis in *Nicotiana tabacum*, which produces 3- and 4-aperturate pollen grains. It appears first, that both pollen types are not distributed at random in the anther. Pollen grains with 4 apertures are located in the medium part of the anther whereas 3-aperturate pollens are present all along the anther. Secondly, with two pollen morphs, five different combinations of the four tetraspores are possible. All these combinations were observed in non negligible proportions but homogeneous tetrads are over-represented.

These two important points suggest that constraints act during pollen morphogenesis allowing only a certain range of possible forms. We are trying to understand what are these constraints, what are their nature, when and how they act. We hope that these ontogenetic studies will provide valuable insights into the interpretation and understanding of pollen morphology diversity.

A Sensitivity Approach of Character-type Weighting and Species Sampling Allows to Resolve Conflicts in Molecular Phylogenetic Analyses

Michel C. Milinkovitch, Jun Adachi, Rick LeDuc, Frederic Farnir,

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Michel Georges and Masami Hasegawa.

Phylogenetic analyses based on 1,352 base pairs of two mitochondrial ribosomal genes and of the mitochondrial cytochrome *b* gene for all major groups of cetaceans contradicted (Milinkovitch et al. 1993, 1994) the classic taxonomic division of cetaceans into two highly divergent clades: the echolocating toothed whales (Odontoceti) and the filter-feeding baleen whales (Mysticeti). Indeed, maximum parsimony (MP), maximum likelihood (ML) and neighbor joining (NJ) analyses of these multiple gene fragments suggested that one group of toothed whales, the sperm whales, forms the sistergroup to baleen whales (Milinkovitch et al. 1993, 1994).

Based on a full cytochrome *b* data set, Arnason and Gullberg (1994) suggested that dolphins and mysticetes form a clade to the exclusion of sperm whales, and hence, challenged both the traditional hypothesis of toothed whale monophyly and the Milinkovitch et al.'s hypothesis of sistergroup relationship between sperm whales and baleen whales.

Several reanalyses of Arnason and Gullberg's data set suggested that the grouping of dolphins and baleen whales in a clade was an artefact due to (1) saturated transition substitutions (Milinkovitch et al. 1995, Milinkovitch, 1995a, 1995b) and (2) dependence of the outgroup choice (Adachi and Hasegawa 1995). Although these reanalyses of Arnason and Gullberg's data yielded an overall support for the hypothesis (Milinkovitch et al. 1993, 1994) of sistergroup relationship between sperm whales and baleen whales, it is indisputable that MP and ML analyses of the cytochrome *b* data set yield a tree which topology is very dependent of species sampling and weighting of character types. Using an extended full cytochrome *b* data set, and assuming that a bootstrap value is a reasonable indicator of support of an hypothesis, we present here a sensitivity analysis testing exhaustively the influence of important parameters on the topology of the resulting trees and on the bootstrap values supporting the three alternative phylogenetic hypotheses. All 1484 combinations among the five following parameters are tested: method of character analysis (DNA-MP or DNA-ML or protein-ML), character-type weighting (5 different weighting schemes tested in MP analyses), choice of ingroup species, choice of outgroup species, use of a single or of two artiodactyl outgroup species.

Morphological vs. developmental complexity in centipedes

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Two different post-embryonic developmental schedules are known in Chilopoda. Lithobiomorpha and Scutigleromorpha develop through hemianamorphosis, i.e. by se addition of segments during a few larval stages, followed by further postlarval mo without segment increase. On the contrary, Scolopendromorpha and Geophilomo develop epimorphically, hatching with the final complement of segments. We analy segmental variation of metric characters such as sternite length and width to expl structural plasticity and complexity and their possible relationship to post-embryo developmental complexity in representatives of the main clades of Geophilomorpha. T models were compared. In the first (family Mecistocephalidae) the number of b segments is invariably fixed within the species and identical between sexes; in the o more common model (all remaining families) genetically controlled inter- and intra-differences occur. We found that size and shape of individual segments are not specified their absolute serial position, but globally affected by their relative position along trunk; that is, segments do not behave as unit homologues. During the most part of p embryonic development, we found no sizeable increase of structural complexity; that the segmental patterns of adults overlap those of juveniles. Within species and s individuals belonging to a cohort with more trunk segments have larger overall si surprisingly, however, that is not just because of the larger number of body units, but e more so because of the larger average size of individual body parts, including both segments and the segmentally invariant fore and hind body ends. All major determinan adult differences, both intra- and interspecific, seem to be laid down very early development, possibly as a consequence of different size (cell number?) of (pre)segmen anlagen.

Several traits, especially of the dorsal and lateral aspects of the trunk, are suggestiv higher morphological complexity of Lithobiomorpha in comparison with Geophilomo This is in agreement with a widespread behaviour among arthropods, where struc complexity along the longitudinal body axis is generally matched by, although not caus dependent on, developmental complexity in the time dimension.

COMPETITION AND THE MAINTENANCE OF GENETIC DIVERSITY IN *DAPHNIA MAGNA* POPULATIONS

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Pairwise competitive interactions were investigated between six clones of *Daphnia magna* originating from two populations. Ten neonates from two clones were used to inoculate 1L cultures which were maintained at 20°C and low food conditions (1mgC/L/3days) for eight weeks. Ephippia were removed and counted during and at the end of the experiment. The population size and composition was established on completion, clones being identified by allozyme electrophoresis. Life history parameters were also obtained for the clones, from which the intrinsic rate of population increase, r , was calculated.

The experiment led to unexpected results. A competitive hierarchy could not be established, although clones from one population always outcompeted clones from the second; r did not predict the outcome; the outcome did not relate to observations from the field: a rare clone outcompeted or coexisted with dominant clones. The results are discussed.

The Red Queen hypothesis (Van Valen, 1973) implies that improvement of each species altered the environment for the other members of the community. In stable ecosystems the relative state of adaptation in all interacted populations must increase continually and nearly in the same rate. Rate of progress on each stretch of time is setting by the species which can changing most rapidly. The main embarrassment in model' application to real ecosystems is how to choose the sophisticated measure of improvement rate in different taxa and living forms. For such case the share of energy flow down through the species population in per cent of hole primary production in the ecosystem might be useful. Variations of the energy flow on the appropriate time scale shows the alteration in the relative state of adaptation. According to this criterion, the "speed of race" in modern biosphere defined by Homo sapiens population consuming the largest part of primary production of land ecosystems. The volume of removed production grows up on exponent. Following ecosystems transformation might be described as a artificial restraining of natural successions for benefits in primary production. In spite of biocenotic changes in communities structure, the large-scale ecosystem transformation causes some evolutionary consequences.

The rate of anthropogenic transformation in modern ecosystems defined now by a species exempting from biocenotic control. Human population growth is still independent from ecosystems quality and species composition. Feedback loops in such systems are absent. As a result, all members of human impacted ecosystems may only participate in a chase for rapidly altered environment, including the adaptation to new food sources producing by mankind. The speed of these changes divides all species in two groups according to the duration of live cycles and fruitfulness. Adaptations in rapidly propagated species with short life-time may occurring on all levels including physiological and morphological adaptations and may be strengthened by selection on genetic level. Well-known cases of insecticide tolerance in many insects shows this kind of improvement. In large vertebrates with long duration of life this way is prohibit. The only possibility for them is in behavioral adaptations, many visible examples of which have been noticed in urban populations as well as in high productive artificial ecosystems. Because of increasing of transformation rate, the border divides these two strategies continuously dropping and for a lot of species this race becoming a wild-goose chase with the extinction at the end.

A meta-analysis of the heritability of developmental stability. A. P. Møller and R. Thornhill, Department of Population Biology, Copenhagen University, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark; Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131, USA. 240 ITG

The existence of additive genetic variance in developmental stability has important implications for understanding of morphological variation. The heritability of fluctuating asymmetry as a measure of developmental stability has frequently been estimated from parent-offspring regressions, sib analyses or from selection experiments. We review by meta-analysis published estimates of the heritability of one measure of developmental stability, the degree of fluctuating asymmetry in morphological characters. The overall effect size of heritabilities of fluctuating asymmetry was 0.16 from 26 studies of 13 species, differing highly significantly from zero ($P < 0.0001$), which indicates that there is a significant additive genetic component to developmental stability. Effect size was larger for selection experiments than for studies based on parent-offspring regression or sib analyses, implying that genetic estimates were unbiased by maternal or common environment effects. Additive genetic coefficients of variation for fluctuating asymmetry were considerably higher than those for character size per se. Developmental stability may be significantly heritable either because of strong directional selection, or fluctuating selection regimes which prevent populations from achieving a high degree of developmental stability to current environmental and genetic conditions.

MONTALVO, ARLEE M., SUSAN G. CONARD, and M. T. CONKLE. USDA P1
Forest Service, Pacific Southwest Research Station, Riverside,
CA, 92507, USA. Population Structure and Clonal Variation in
Quercus chrysolepis Liebm. (Fagaceae).

Information about genetic structure and reproductive ecology is important in developing forest management policies that will maintain the long-term viability of populations. Stands of wind-pollinated canyon live oak (*Quercus chrysolepis*) are maintained for fire management and as habitat for wildlife. Trees resprout in response to fire and stands frequently include groups of visibly connected trees. We determined the extent to which these clusters are clonal and defined the spatial pattern and diversity of genotypes for populations in the San Bernardino Mountains in southern California. We mapped over 100 trees at each of five sites and genotyped each tree for 7 allozyme loci. We detected an average of 34.4 ± 7.3 (s.d.) clones and 33.4 ± 7.2 genotypes per site. Clone formation and the finding that most clones consist of few trees was confirmed by the very high spatial autocorrelation of multilocus genotypes at short distances. However, clone size increased significantly with increased individual heterozygosity, suggesting that the long-term integration of selection over time favors highly heterozygous clones. Ecological estimates of clonal diversity and evenness were high relative to reports for most other clonal species; an average of 97% of clones had distinct genotypes and Simpson's index of diversity averaged 0.95 ± 0.02 . Population genetic analyses of clones from six sites (319 clones) also revealed high genetic diversity within sites (mean $H_S = 0.403 \pm 0.085$). Only a small proportion of total genetic diversity was explained by variation among sites (mean $G_{ST} = 0.017$) and we found even less substructure within sites (G_{ST} for plots relative to site was 0.007 and 0.001 for the two sites examined). Moreover, fixation indices (F within sites) were generally small and positive, suggesting that little inbreeding occurs. These patterns are consistent with studies of other tree species that are highly outcrossing and wind pollinated. Resulting estimates of gene flow were high, increasing with proximity of subpopulations ($N_m = 10.1$ among sites, while $N_m = 19.9$ and 200.7 among plots at two sites, respectively). Despite this, spatial autocorrelation analysis of clones indicated fine scale genetic structure at distances under 4m, possibly due to limited seed dispersal.

POPULATION STRUCTURE OF WILD RABBIT IN IBERIAN PENINSULA PI

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The european rabbit *Oryctolagus cuniculus* is originating from Iberian peninsula. The first remains of the genus have been found in south of Spain 6 million years ago. Its expansion through north of Spain and south of France seems to be a natural process while its conquest of other parts of the world is closely related to human activity. Consequently, studying the population structure in Iberian peninsula is of great interest to understand natural movements of this species.

Previous studies on mitochondrial DNA (mtDNA) have lead to the recognition of two maternal lineages called A and B. The first one has been described in south of Spain and the second in north of Spain and France. The repartition of nuclear alleles strengthens the idea of a clivage between south and north of the peninsula : the diversity in the north is much lower than it is in the south with diagnostic alleles for each area. Results on protein polymorphism also support the strong social structure of wild rabbit previously described.

A network has been created between several laboratories, the aim of which is to characterize the same populations with various tools : mtDNA, protein polymorphism, immunoglobulin and morphometry.

We present a joint study of populations from Portugal based on the analysis of protein polymorphism and mtDNA. The sampling covers quite uniformly the country as well as one Azorean island.

All the populations studied present the mtDNA type A and nuclear alleles characteristic of Southern populations with two exceptions: Bragança in north-east and Vila Viçosa in center-east. Rabbits from Vila Viçosa are exceptionnal in that they present mtDNA type A or B depending on the individuals. These two types are observed in the samples from Bragança and the population also appears heterogeneous for the nuclear alleles: alleles diagnostic for Northern populations are found in addition to that of Southern populations.

The hypothesis of a hybrid zone will be discussed.

Sociality and the rate of evolution in mitochondrial and genomic DNA

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Eusociality causes by definition reproductive hierarchies within the society (Wilson 1971). As a direct consequence, the genetic effective population sizes N_e are expected to be smaller in social than in solitary species. However, in male haploid social Hymenoptera queens often multiply mate which can counteract the reduction of the overall reduced N_e in social species. Polyandry causes a bias between the male and female contribution to N_e resulting in a larger effective size in the male than in the female sex. Cole (1983) argued that the degree of polyandry increased with increasing nest size. Large nests are usually found in the socially most advanced Hymenoptera. Polyandry in highly social insects should cause differences in the evolutionary rate of the mitochondrial and nuclear genome if genetic drift is a significant parameter for molecular evolution. We used sequence data of the nuclear 28S rDNA (D2 region) and the mitochondrial 16S rDNA (mtDNA) of various social and solitary wasps (Vespidae). The average substitution rates in the mtDNA and the nuclear DNA were almost equal in solitary Eumenidae. With increasing nest size, however, the substitution rate in mitochondrial DNA was significantly larger than in nuclear DNA. The substitution ratio (mtDNA/nuclear DNA) was almost twice as high in social Stenogastrinae and Polistinae. The substitution ratio was about 4.6 in ten eusocial Vespinae species, and exceeded 15 in two extremely polyandric *Apis* species. Genetic drift through extreme bottlenecks in the mitochondrial DNA pool, and/or the larger effective genomic population size in relation to the mitochondrial effective size, serves as a plausible reason for these phenomena.

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Crawling behaviour in *Macoma balthica*: the parasite-manipulation hypothesis revisited

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Macoma balthica is a common infaunal tellinid bivalve that throughout most of its North Atlantic distribution range has been observed to make conspicuous often U-shaped crawling tracks on the sediment surface in intertidal habitats. Since previous studies have shown that crawling *Macoma* inevitably are infected by digenic trematodes, in contrast to burrowed specimens, the behaviour is presently considered a parasite-induced behavioural change inflicted by the parasites to promote their transmission via predation to various waterbirds acting as final hosts. Although attractive, this manipulation hypothesis has, however, not yet been properly evidenced. The aim of the present study was, therefore, to elucidate whether also other parameters than parasite infection are able to explain the observed behavioural dichotomy.

Crawling and burrowed *Macoma* were collected on an intertidal flat in Lisia Bay in the White sea, Russia. The two behavioural categories were compared regarding age, size, sex-ratio, condition, growth rate, intestinal content, and parasite prevalence. Of those parameters sex-ratio, intestinal content, and growth rates differed significantly between crawlers and burrowers. Crawlers comprised more females, expressed lower growth rates, and contained a higher amount of organic components within their gut in comparison with burrowers. As evidenced by the absence trematode infections in the studied population of *Macoma*, it was concluded that crawling behaviour is not necessarily trematode-induced in contrast to common belief. It is argued that crawling *Macoma* represent a group of retarded animals that optimize deposit-feeding and consequently are engaged in frequent relocation to encounter unexploited food resource on the sediment surface.

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Were the first organisms heat engines? A new paradigm for the origin of life and early evolution. Anthonie W.J. Muller. Dep. of Geology and Applied Geology, University of Glasgow. At present most of the ATP consumed by living organisms is generated by Mitchells chemiosmotic mechanism: respiratory or photosynthetic enzymes pump protons across a membrane, building up a voltage and pH difference across it as a high-energy intermediate, and the high-energy protons return through the F_0F_1 ATPsynthase. In a proposed simple forerunner of the mechanism, which works on continuous light-dark cycling, a membrane voltage is generated by light-induced dipoles which decay in the dark. A simpler forerunner uses thermal cycling: a thermotropic phase transition of the membrane lipids results in a high membrane dipole potential. The most simple forerunner does not need a membrane at all: in a precursor of the F_1 moiety of ATPsynthase the catalytic ATP-synthesizing cycle is synchronized with a thermal cycle. These thermal-cycling based forerunners are essentially heat engines. In an origin of life model constructed with these forerunners:

- (1) Proteins come first, nucleic acids come later;
- (2) The first enzymes have general condensing capability: they can catalyze peptide bond formation just as well as phosphorylation;
- (3) A small fraction of the resulting polypeptides have the same general condensing capability: the enzymes therefore can propagate, albeit not very efficiently;
- (4) Thermal cycling occurs when the enzymes are carried along by a convection current; the convection cell constitutes the self-organizing dissipative structure required for the origin of life; convection occurs in natural waters such as volcanic hot springs;
- (5) Present day requirement of thermal cycling, for instance during induction of germination, division, flowering, budding, is interpreted as possible relic of early thermal cycling;
- (6) Present day regulation by Ca^{2+} , phosphorylation, and heat-shock proteins is interpreted as a method for mimicking early thermal cycling during isothermal conditions.

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Genetic and ecological differentiation in a transition zone of two closely related *Gammarus fossarum* forms.

A transition zone between two genetically distinct *Gammarus fossarum* forms was investigated by allozyme electrophoresis. Syntopic populations consisting of both *Gammarus fossarum* forms are frequent along the river Rhine, that is supposed to be a migration barrier for this species. Parallel clines of the allele frequencies indicate secondary contact of formerly isolated *Gammarus fossarum* populations.

However, hybridization in our studied area of overlap seems to be rare. Therefore, a dynamic equilibrium of continual immigration from outside the sympatric zone and exclusion by competition inside the zone is suspected. Some ecological differentiations between the two closely related forms were found. While co-occurring equally in most habitats, one of the forms predominates in spring brooks. In addition, differential temporal fluctuations in abundance and sexual activity was found. Thus the strength of competition is weakened and the duration of coexistence could be extended.

'HAYSTACKS' AND 'ISLANDS': HIERARCHICAL LEVELS OF SPATIAL STRUCTURE AND THEIR CONSEQUENCES FOR THE EVOLUTION OF SEX ALLOCATION IN MITES AND OTHER ARTHROPODS

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Evolutionarily stable (ES) sex allocation strategies depend critically on how the population is structured with regard to competition for mates and resources. This structure is determined by spatial heterogeneity, dispersal and colonization behaviour. In mating groups lasting one generation where dispersal is by mated females, female-biased sex ratios will be favoured by 'local mate competition', especially when the number of foundresses is small. When groups last several generations before dispersal takes place ('haystack' structure), local relatedness develops and this can favour an extra female bias. However, when groups are permanent with some dispersal in each generation ('island' structure), relatedness builds up without an effect on sex ratio bias because competition also takes place within groups. Current models of evolution under a haystack structure generally assume (1) unlimited growth for a fixed number of generations (and hence no local density dependence), (2) absence of substructure, and (3) sex ratios that are inflexible over generations. These assumptions will often be unrealistic. In this presentation I demonstrate by simulation that, although local density dependence in the haystack population diminishes the sex ratio bias, strongly female-biased sex ratios can still develop when foundress numbers are low. It is also shown that substructure in the haystack by subdivision into one-generation mating groups promotes the female bias. Finally, it is shown that the ES sex ratio can change radically with generations within haystacks. When population growth is density dependent, the sex ratio of the last generation should be more female-biased than in the preceding generations. In the case of haystacks subdivided into local mating groups, the sex ratio in the first generation should be less female biased than in the following generations. It is argued that a haystack structure is frequently found among small arthropods with a colonizing life style and that subdivision into one-generation mating groups may occur, e.g., among plant-inhabiting mites. To illustrate these points, predatory mites of the family Phytoseiidae are considered in more detail. Some species are found to exhibit a stronger female bias than expected from local mating competition alone. This extra bias may well stem from selection in a haystack structure. These species have highly subdivided, locally unstable populations. Other phytoseiid species have a life-style that leads to more permanent subpopulations that have an island-like structure. As predicted, these species generally show less female-biased sex ratios.

Is the highly polymorphic Vegetative Incompatibility system selectively neutral?

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Fungi have the possibility to fuse without the interference of sex. In natural populations, however, vegetative incompatibility (VI) normally prevents this fusion. Genetical studies have shown that VI is genetically determined and that it is highly polymorphic. A large number of loci exist, with (usually) two alleles each. One allelic difference normally causes incompatibility.

In an attempt to explain the evolution of this polymorphic system, several population genetic models have been studied. A comparison of models with different selective regimes and a neutral model showed that selection is probably not the main factor in determining the polymorphism. In large fungal populations random genetic drift and mutation may offer sufficient explanations.

Vegetative incompatibility is compared with other highly polymorphic incompatibility systems. A test for the neutral hypothesis in natural populations of asexual species will be discussed.

Genetic structure of European populations of Atlantic salmon (*Salmo salar* L.) inferred from RFLP analyses of PCR amplified mitochondrial DNA.

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Throughout its range, Atlantic salmon (*Salmo salar* L.) exhibits large interpopulational genetic differences. These differences have been attributed to restricted gene flow among populations caused by efficient homing. Subdivision increases the role of genetic drift but also facilitates local adaptations.

We studied the genetic relationship among eight populations of Atlantic salmon using RFLP analyses of PCR amplified mitochondrial DNA segments. Six different haplotypes were detected by restriction analyses of the NADH dehydrogenase 1 segment, employing four endonucleases. Most haplotypes were distributed throughout the study area, which implies extensive gene flow and/or that the genetic differences between individual haplotypes predate the last glaciation. Significant genetic differentiation was observed among populations. No correlation was found between genetic and geographical distance among populations. A hierarchical analysis of the distribution of the mtDNA variance revealed that only a very small part of the variance was distributed among geographical groups within the study area. The effective migration of females (N_m)_F between rivers was estimated to be approximately 1 per generation.

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We address the evolution of cannibalistic behavior among individuals during larval period in temporary populations of discrete generation in the view of parental manipulation. Parent controls the occurrence of cannibalism of her offspring so as to maximize her fitness. We focus on size variation as key factor that induces cannibalism. We consider the most conservative condition of invasion of cannibalistic trait into the population; size variation is generated only by demographic stochasticity, and there is no kin recognition ability. We assume that there is a scalar property between mean (μ) and variance (σ^2) of body size in population through the developmental period, $\sigma^2 = c\mu$, where c is a constant. The fitness of individual without cannibalizing other conspecific increases compared with the fitness of individual without cannibalizing (figure 1). We suppose that larvae randomly meet each other and cannibalistic individual eats conspecific one if its opponent is smaller than its body size.

Intuitively, when the trait group consists of large number of clutches, cannibalistic trait can invade because that cannibal rarely eats relative. We analyze invasion condition of cannibalistic trait with respect to clutch numbers (m) and the parameter that expresses degree of size variation through developmental period (c). The condition that the parameter of degree of size variation (c) is small, the numbers of clutch permits invade cannibalistic trait is small compared with in the condition that parameter of degree of size variation is large (figure 2). The invasion condition is satisfied earlier in the developmental period in population that consists of large number of clutches than in population that consists of small number of clutches. Furthermore, cannibalism would occur earlier in the case that parameter of size variation (c) is larger than in the case that parameter of size variation is small, when invasion condition holds in the both cases (e.g. $m = 25$).

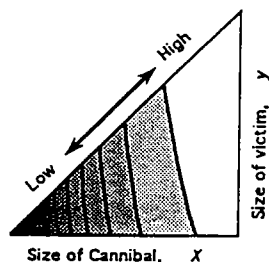


Figure 1 The contour plot of individual fitness of size x that eats conspecific victim size y .

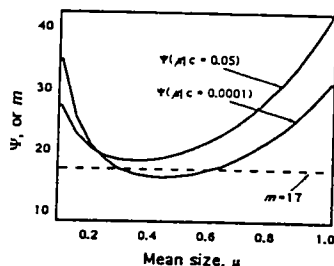


Figure 2 Function Ψ determines the invasion condition of cannibalistic trait into population. The horizontal dashed line shows numbers of clutches. When the value of Ψ is below the line, the invasion condition of cannibalistic trait holds.

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Locomotor activity in selection lines of *Drosophila melanogaster*.

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Locomotor activity is known to be a very complex behavioral characteristic of *Drosophila*. The performed experiment will try to give insight in the relationship between this behavioral trait and morphological features.

Flies of selection lines on wing length are tested in a locometer. Results are given in terms of locomotor activity, wing length and weight. Weight and thorax length are recognised as correlated characters. It will be tested whether differences occur between the separate selection lines and whether (cor)relations can be found between the three measured traits.

A molecular & morphological investigation of the large arionids (Mollusca: Pulmonata) of N-W Europe: identifying friend & foe.

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Some large arionid slugs are now considered to be important agricultural pests in many areas of Continental Europe, where 'slug plagues' have become a common phenomenon. However, identification of arionid taxa is problematic, complicated by common colour varieties and morphology, confounding attempts to map their distribution and differentiate pests and non-pests. We have used a PCR-based molecular approach combined with anatomical investigations, first as an aid to identification and subsequently as a tool for investigating the ecology and reproductive strategies and phylogeny of this group. Our evidence suggests that the large arionids are divisible into four distinct groups, of which three appear capable of generating pests, distinguishable from their congeners on the basis of reproductive strategy and life-history strategy.

Using this integrated approach we have produced a concordance between colour varieties and taxon, allowing use of varietal distribution records from the early 19th Century to the present day. Combining these data with our own pan-European survey has made it possible to identify the rapid, recent advance of some taxa throughout the U.K. Their life-history and colonization profile closely parallel those of more strictly Continental species shortly before they began to produce major outbreaks and became serious agricultural pests, suggesting that these taxa deserve further attention from agriculturists. Future studies may be assisted by the taxon-specific molecular markers we have identified.

The amplification and characterisation of cholinesterase-like gene in various organisms

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The human neurotransmitter enzyme gene, butyrylcholinesterase, has no known physiological function in humans and yet, has previously been shown to be conserved among some closely related vertebrates. The work described here extends this finding across a much wider range of species, carried out at the level of DNA sequence variation.

PCR with degenerate primers based on the human butyrylcholinesterase DNA sequence, were used to amplify up a region which included the invariant serine residue found at the active part of the enzyme. This region is expected to be under evolutionary pressure to maintain sequence homogeneity, yet allowing sufficient substitution over the evolutionary distances covered to amplify cholinesterase-like genes in a wide range of organisms.

By the use of low stringency conditions for the PCR reaction, products could be observed in most of the organisms tested. The products were then cloned and 21 samples were successfully sequenced. The sequences from the various organisms were then aligned with respect to the human butyrylcholinesterase DNA sequence. Phylogenetic trees were then derived from this alignment by several different computational methods.

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The effective size of spatially structured populations.

Many natural populations exhibit significant genetic subdivision and, in order to understand the long-term genetic behavior of such populations, we need to understand how their spatial structure influences their effective size (N_e). One problem in addressing this issue has been confusion over the relationship between N_e and neighborhood size. I have examined, both analytically and through simulation, how neighborhood size influences the effective population size. A decrease in the neighborhood size reduces N_e , but, in general, the effect is small. A second problem arising when there is genetic substructure is the potential for bias in the estimation of N_e from genetic data. These conditions violate the usual assumption of panmixia and an incorrect sampling strategy will result in N_e being consistently underestimated.

EVOLUTION OF DIFFERENT GALL TYPES IN WILLOW-FEEDING SAWFLIES (HYMENOPTERA: TENTHREDINIDAE)

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The sawflies that feed on the plant family *Salicaceae* can be divided into seven informal groups based on larval feeding habit or gall type: 1) free-living larvae, 2) leaf folders, 3) leaf galls, 4) midrib galls, 5) petiole galls, 6) stem galls, and 7) bud galls. Each gall type can be found on several willow species. In folders and galls the fold or gall formation is caused by substances secreted by the female during oviposition. It has been proposed that the galling habit evolved from free-living larvae via leaf folders, and that the different gall types evolved gradually in the sequence mentioned above. Thus, the galling site would have "wandered" from the leaf margin towards the stem as a result of gradual changes in oviposition site preference. Radiations to different willow species would have occurred after the evolution of new gall types.

Representative species from the genera *Nematus*, *Pontopristia*, *Decanematus* (all with free-living larvae), *Phyllocolpa* (leaf folders), *Pontania* (leaf blade and rib galls) and *Euura* (midrib, petiole, stem and bud galls) were chosen for an allozyme study. Eight informative enzyme loci were surveyed, and a phylogenetic analysis was conducted. The loci were considered as characters, and step matrices were used to define the cost of transformations between different character states (allelic combinations). *Nematus pavidus*, *N. salicis*, *Pontopristia amentorum* and *Decanematus viduatus* were used as outgroups.

Preliminary results suggest, that: 1) indeed leaf folders seems to be a basal group, and 2) leaf galls evolved subsequently, but 3) after leaf galling had evolved, new gall types evolved in a less predictable pattern. We suggest that after the gall forming habit evolved, radiations to free "galling niches" occurred many times. More data are however needed for firmer conclusions.

Use of random amplified polymorphic DNA (RAPD) markers for genetic analysis in the Genus *Barbus* (Cyprinidae)

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The random amplified polymorphic DNA polymerase chain reaction (RAPD-PCR) is a recently developed technique that involves the amplification of random fragments of genomic DNA. This method has been successfully applied to strain identification, genetic mapping, etc. in a variety of organisms.

The goal of our study is the phylogenetic analysis of the *Barbus* species through the use of RAPD-PCR. The genus *Barbus* (Cyprinidae) is a very important freshwater group in the Iberian Peninsula. This genus presents a special evolutionary interest due to the involved taxonomic polemic and its endemism in our country.

The data we are introducing represent preliminary results in our research. We have examined the multiple band profiles in three species (or subspecies?): *B. sclateri*, *B. bocagei* and *B. graellsii* by using 20 primers (Operon Technology kit C). For each primer evaluated we have scored from three to five major bands to two or three minor bands. These fragments range in size from 100 to 2500 bp. approximately.

The amplified fragments obtained in these three groups are very similar in their number and size. Thus, these first results seem to indicate a close phylogenetic relationship among the three analysed groups, that, probably, does not justify the taxonomic classification into different species. However, more data are needed to reach a definitive phylogeny.

Isozyme, RAPD and mtDNA differentiation in geographically distant populations of *Ceratitis capitata*

PiG

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Ceratitis capitata is a polyphagous and multivoltine species that infests more than 250 varieties and species of commercial fruits. Despite its economical importance, very few attempts have been carried out in order to assess different aspects of the genetic structure of its populations.

Thus, we have analysed three samples of *C. capitata* from distant localities of Spain, Málaga (South), Madrid (Centre) and Valencia (East), by means of three different approaches: the analysis of 25 isoenzymatic loci, 226 RAPD markers obtained with 14 random primers and RFLPs in mtDNA by using 22 restriction endonucleases.

The results we have obtained with these three techniques are highly congruent and showed up that a great level of geographic differentiation exists in our populations, as $F_{ST} = 0.1889$ from isozyme data, or $N_{ST} = 0.2462$ from mt DNA data. The average similarity value obtained from RAPD markers, 0.3941, also reflects a high differentiation.

Levels of gene flow were calculated based upon these indexes, or the private alleles method, and no significant gene flow was detected between any of these populations.

The existence of selective forces acting on these populations and promoting adaptation to specific environmental conditions as well as the absence of significant gene flow could be the main reasons of this geographic differentiation.

Frequency and Density Dependent Fitness Experiments in the Wheat Mildew Fungus

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Powdery mildew is an economically important disease of cereals. It is caused by the biotrophic fungus *Erysiphe graminis*, which grows as asexual colonies on the leaves. Recent work has focused on the effect of the density of colonies on the dynamics of mildew epidemics. Empirical work has shown that life history traits are affected by density (e.g. Stähle, 1986, Carver & Ingerson-Morris, 1989), but it had not been established whether this could cause selection between isolates.

Tests were carried out to investigate whether density and frequency could affect selection. No evidence for frequency-dependent selection was detected. However, density did have an effect on the coefficients of selection. The effect of density was investigated further by looking at how selection changed over a range of densities, and some simple life history traits were examined to investigate which stage of the life cycle of the fungus was being affected by density. The effect of density dependent selection on the population structure of the fungus will be discussed.

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Stähle, U. (1986) *Z. Pflanzenkrankh. Pflanzenzucht.* **93**: 172-6

Why have the diving birds been heavily victimized by oil pollution ?

p 4

-Aspect of an evolutionary adaptation in nutritive depot structure of diving birds-

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Many seabirds have been victimized by oil pollution on the sea and most of them were known to be diving birds. In the southern Japan Sea the illegal oil spill victimized an estimate of 4600 seabirds in January 1986 and 76 % of the dead birds counted were a diving Alcid, rhinoceros auklets (*Cerorhinca monocerata*) and oil spills have continued victimizing this family along Japanese Islands. Oil was attached to all the auklets with the weight ranging from 4 % to 65 % of the body weight with an average of 31 %, however, they did not intake the oil with the exception of several individuals. This means that auklets did not die from the oil poisoning but from other cause. We studied the reason of the high dead ratio of this family by the nutritive analysis, using 59 rhinoceros auklets (44 oil-polluted dead, 2 natural emaciated and 13 fishery accidentals).

Oiled auklets were all in mal-nutritive condition in their muscle weights, muscle lipid weights, body lipid weight, femur marrow water weight, similarly emaciated as in auklets of natural death. This showed that they died from starvation, for their losing ability to pursue prey marine animals. Even in healthy conditions, the level of lipid reserve of this auklet was lower than the other family, such as Procellariiforms, which adapted for aerial flight. On the contrary, the skeletal and pectoral muscle weights (for body weight) of this auklet were heavier than Procellariiform birds. The family Alcidae has adapted for aerial and submerged flight with propelled wings. They developed large pectoral muscles as well as the large sternum to support its volume, which also play the important role to prevent the internal organs from the damage when diving from the air and the hydraulic pressure when submerged up to 60m depth from the water surface. This heavy bodily composition can be attributed to this species' adaptation for deep water foraging, while the low lipid reserve may suffice their underwater foraging restricted to local, and non-migratory movements. Owing to this low lipid reserve, when victimized by oil-pollution of the sea, the alcid species tends to quickly fall into mal-nutritive condition and may die in short periods.

Extreme genetic homogeneity in a cyclically clonal freshwater bryozoanB. Okamura¹, C.S. Jones² & L.R. Noble²¹School of Biological Sciences, University of Bristol, U.K.²Department of Zoology, University of Aberdeen, U.K.

Organisms ranging from corals to trees include prolonged periods of clonal reproduction in their life cycles. Such organisms, however, generally undergo a sexual phase which generates genetically diverse offspring. Life histories that combine both asexual reproduction with occasional outcrossing offer the advantages of both reproductive modes: clonal reproduction avoids the cost of sex and allows the proliferation of highly adapted genotypes, while occasional sex provides genetic variation for both clonal specialization and avoidance of local extinction. Cyclically clonal organisms, such as *Daphnia*, conform to these expectations in having high levels of clonal diversity and evidence of local adaptation and persistence. Here we describe a system that apparently does not conform.

Colonies of the bryozoan, *Cristatella mucedo*, are commonly found in temperate lakes and ponds. Like *Daphnia*, *C. mucedo* incorporates a high degree of clonal reproduction with occasional outcrossing. Genetic characterization (via RAPD PCR) of local populations in southern England has revealed extreme clonality and high levels of relatedness both within and between populations. Thus populations of *C. mucedo* in southern England are composed of a small number of highly-related clonal types. Genetic analyses also revealed that sexuality generates little significant variation. Thus, although larvae are the result of outcrossing (and not selfing), little genetic variation is produced in such clonal populations. Ecological data indicate relatively frequent within-site extinction and colonization suggesting significant rates of dispersal amongst lakes and ponds. Spatial and temporal escape from enemies mediated by dispersal and colonization may explain how such genetically homogeneous animals can persist in the landscape of southern England.

THE EVOLUTION OF MIGRATION AND OTHER LIFE-HISTORY TRAITS :
THE METAPOPOPULATION EFFECT

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A Markovian extinction model that takes into account age-structure of local populations, allows consideration of the effects of demography on the evolution of migration and reproductive effort. It is shown that ecological succession and unequal local extinction rates strongly affect the ESS dispersal rate. Polymorphism between genotypes with different migration rates can be maintained, but are not evolutionarily stable. We show that, at equilibrium, while migrants genotypes are selected for at colonization, each population evolves towards fixation of the less-migrating genotype. It is shown that in most cases there is an optimal migration rate, which maximizes the metapopulation size. Because of the two-level selection, the ESS is always lower than the optimum dispersal rate. It is shown that, under some circumstances, environmental changes may lead the metapopulation to global extinction, even though the new environment could in fact host a viable metapopulation.

The same model is used to study the evolution of reproductive effort with a hypothesis of density-dependent juvenile survival, and density-independent adult survival. For a given migration rate, polymorphisms between annual and perennials, but not between two perennial genotypes, can be maintained. At equilibrium, while the high-fecundity genotypes are selected for at colonization, each population evolves towards fixation of the more perennial genotype. When the ESS is a perennial type, the best strategy of resource allocation to reproduction is a simple function of the local extinction rate and of the trade-off curve between fecundity and adult survival. There are interactions between migration and reproductive effort, such that increased adult survival selects for increased dispersal, and that increased dispersal selects for increased allocation to adult survival. This last result is related to the fact that the optimal (maximizing metapopulation size) dispersal rate is larger for perennial than for annuals. Predictions of the model are extended to the evolution of dormancy, diapause and host-parasite interactions, and compared with published data.

Microsatellite mutation mechanisms in artiodactyls: allele sequence differences within and between species

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It is generally assumed that simple strand slippage is the prevailing mutation mechanism at microsatellite loci, resulting in allele frequency distributions where alleles seem to differ from each other by the number of repeats. For characterizing variation within species (microheterogeneity) and between species (evolution of microsatellite loci) we sequenced several cattle (*Bos taurus*, *Bos indicus*), sheep (*Ovis aries*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*) and reindeer (*Rangifer tarandus*) microsatellite alleles from four loci. Between-species differences were mainly small deletions and insertions of the flanking sequences as well as substitutions, mainly transitions. In Cervidae the microsatellite block was shorter and involved more interruptions than in Bovidae. The degree of similarities of flanking sequences between species were consistent with the known phylogenetic relationships of the species at all loci. In cattle (several breeds and races studied) significant microheterogeneity (base substitutions in the microsatellite block and hidden alleles as a consequence of length variation in different repeat blocks) was observed at three loci. At one locus the sequenced alleles fall into three distinct classes on the basis of both the flanking sequences and microsatellite blocks. In the first class the sequences of the alleles differ from each other, too: certain mutations were characteristic to zebu. In this class the sizes of alleles were based also on deletions and insertions of the flanking sequence, in addition to the microsatellite block. The second class is typical for *B. taurus* breeds only. In conclusion, simple replication slippage as the only mutational mechanism for microsatellites is an oversimplification. Mutations at the flanking sequences are much more common than supposed, as well as base substitutions within repeat block. If this turns out to be a common phenomenon, it has some important implications concerning the applications of microsatellite loci, and their evolution.

Wing load plasticity in *Eristalis arbustorum* (Diptera: Syrphidae).

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Wing length relative to overall body size (wing load) of *Eristalis arbustorum* is influenced by the rearing temperature in the first half of the pupal stage. At lower temperatures the wing load is lower than at higher temperatures where the wings are relatively longer. The wing load of females is less than of males. The response to temperature is nonlinear and the sexes respond differently to temperature. This plasticity can be observed in the field, where wing load is related to the average temperature of two weeks preceding the collection date. A splitfamily laboratory experiment demonstrated genetic variation for the way in which the flies respond to temperature.

What population-genetic models predict about the distribution of haploidy and diploidy

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Sarah Perin Otto

The haploid and diploid phases of sexual life cycles are extremely variable in length, ranging from little development in one or the other phase to equal development in both. The challenge for theories that describe the transition between life cycles over evolutionary time, and specifically the transition between haploidy and diploidy, is to explain this observed diversity. Most theories concerning ploidy evolution have focussed on advantages to diploidy, including protection against deleterious mutations (the "masking hypothesis" Crow and Kimura 1965) and increased rates of beneficial mutations (Paquin and Adams 1983). Population genetic models that predict the evolutionary dominance of diploidy fail, however, to explain the persistence and evolution of substantial haploid phases in many life cycles. More detailed population genetic studies of the masking hypothesis (Otto and Goldstein 1992) and the hypothesis that diploids adapt faster (Orr and Otto 1994) have revealed conditions that favor the haploid phase of the life cycle as well as conditions that favor the diploid phase. Masking mutations allows individuals to survive but thereby allows mutations to persist in the population. In contrast, deleterious mutations are revealed in haploid individuals and are more rapidly eliminated by selection, creating genetic associations that are favorable to haploidy. Tight linkage or various forms of non-random mating (assortative mating, selfing, and apomixis; Otto and Marks 1995) maintain these genetic associations and favor the increase of the haploid phase of a life cycle. With beneficial mutations, diploid individuals carry twice the number of new mutations as haploids, but unless these mutations are completely dominant they have a lower probability of fixation and spread at a slower rate in diploids. Consequently, beneficial mutations favor the evolution of haploidy rather than diploidy when mutations are partially recessive or when genetic associations are slowly eliminated (e.g. with linkage or asexual reproduction). These results suggest that a correlation should exist between mating system and ploidy level, with outcrossing favoring diploid life cycles and inbreeding or asexual reproduction favoring haploid life cycles. This prediction can be tested in groups, such as the Chlorophyta, with extensive variation both in life cycle and in reproductive system.

Population size, inbreeding and disease susceptibility in the *Silene alba* - *Ustilago violacea* pathosystem.

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The influence of population size and inbreeding level on susceptibility of *Silene alba* plants to infection with the smut fungus *Ustilago violacea* was investigated.

In an experimental garden experiment with 100 individuals from each of 20 populations, 1) significant variation among populations in susceptibility, 2) significant variation among populations in the magnitude of the enhancing effect of the fungal infection on flower production, and 3) significant variation in data of first flowering (being one of the components of disease resistance) was found. Contrary to expectations, in none of these cases were the differences in these characters correlated with differences in population size. Furthermore, there was no correlation between disease incidence in the field (the parents) and disease incidence in the experiment (the offspring). Field observations in consecutive years learned that both population size and disease incidence were highly variable over years.

In experiments with 64 inbred lines, covering 5 inbreeding levels per line, inbreeding depression in disease resistance was found in some, but not in other lines.

Overall the results suggest that the interaction between plant and pathogen is not in equilibrium in these populations, possible because of the migration and extinction associated with metapopulation structure.

EVOLUTION OF RESOURCE-CONSUMER COMMUNITY WITH ACCOUNT OF GENETIC STRUCTURE OF CONSUMER POPULATION

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PI

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According to the principle of genetic control, all organism trait values (phenotype) is uniquely determined by its genotype under fixed environment conditions. As a result, the study of frequencies for values of traits in a population reduces to study of frequencies of genes that control the traits under considerations. Let variability of trait values in a population with random mating is determined by one locus with multiple alleles and there are Hardy-Weinberg frequencies of genotypes. Denote by q_i , N , P_{ij} , R the frequency of A_i allele, total population size, individual weight of individual with genotype $A_i A_j$, and resource density, respectively. The model has the following form:

$$\begin{aligned} dq_i/dt &= q_i(w_i - \bar{w}), \quad i = \overline{1, n}, \quad dN/dt = wN, \\ dP_{ij}/dt &= g(P_{ij}, R), \quad dR/dt = h(R) - v(R, q)N. \end{aligned}$$

Here the fitness of i th allele, w_i , equals $\sum_{j=1}^n w_{ij} q_j$, (w_{ij} , f_{ij} , d_{ij}) are fitnesses of $(A_i A_j)$ genotypes with fertilities (f_{ij}) and mortalities (d_{ij}) that depend on individual energy balance integrated in P , $\bar{w} = \sum w_i q_i$ stands for mean fitness. Function g accounts energy expenditures due to individual vital activity and energy influx via resource consumption with trophic functions $v_{ij}(R)$. $v = \sum v_{ij} q_i q_j$. Resource dynamics is determined by its natural growth, h , and consumption $v(R, q)N$.

For this model, the following result is true under supposition of fast (P_{ij}) dynamics:

1. At any stable non-degenerate polymorphic equilibrium with $N \neq 0$ allele frequencies give a maximum to mean fitness.
2. If at this equilibrium $d\bar{w}/dR < 0$, then equilibrium value of R as a function of $\{q_i\}$ reaches here a minimum value.

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EVOLUTIONARY OPTIMAL VALUES OF SWIMMING VELOCITY
AND FERTILITY OF PELAGIC FISHES. CORRELATION BETWEEN
ENERGY EXPENSES FOR VARIOUS KINDS OF VITAL ACTIVITY

A mathematical model of biological community consisting of pelagic fish population and food resource is considered. The model is represented by system differential equations, describing dynamics of fish population density, resource density and body mass of adult female. The dynamics of fish population density is conditioned by the difference between effective fertility and coefficient of mortality. The effective fertility is a proportion of individuals entering into adult cohort at the maturity age onset. Mortality is conditioned by the index of exhaustion, determined as a ratio of body mass of an individual to its normal body mass.

Body mass is a characteristic of energy balance of organism. The energy entering with a food is spent into various kinds of vital activity: basal and active (moving) metabolism, reproduction. Disbalance of energetic flow through organism determines the dynamics of body mass.

Based on the notion Evolutionary Optimal Criteria (EOC), there were determined the evolutionary optimal value of swimming velocity and appropriate body mass of female and number of roes throwing by female of fish for spawning.

The essence of EOC is the following: among population competing for resources and differing by values of traits, survives only one population, namely, that population, whose values of traits provide the maximum to specific rate of growth of population

There was formulated the dependence of above mentioned traits on coefficients accounting the influence of environment. The values of energy expenses on basal and active metabolism and reproduction rate were determined.

In particular, it was shown, that for pelagic fishes the energy expense on basal metabolism is equal to active metabolism plus energy on reproduction. The equilibrium values of fish population density and resource density was determined.

These theoretical results were applied to natural populations of North Baikal omul. There was obtained the satisfactory agreement with the dates of natural observations.

The genetic basis of hybrid male sterility between *Drosophila* sibling species: Rapidly spinning a complex web of epistasis.

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To study the genetic differences that are responsible for the sterility of their male hybrids, we introgressed small segments of an *X* chromosome from *Drosophila simulans* into a pure *D. mauritiana* genetic background, and assessed the fertility of males carrying heterospecific segments of varying size. Although this analysis considered only 20% of the *X* chromosome (roughly 5% of the *D. simulans* genome), and the heterospecific segments were introgressed in only one direction, a *minimum* of four factors that contribute to male sterility had to be invoked to explain the results. In addition, at least two of the factors exhibited a strong epistatic interaction -- males carrying either factor alone were completely fertile, whereas males carrying both factors were completely sterile. Finally, distinct spermatogenic phenotypes were observed for sterile introgressions of different lengths. Males with one category of introgression often managed to produce large quantities of motile sperm, and were observed copulating with females, but always failed to inseminate virgin females. The results suggest that these species have diverged at a large number of loci which have various pleiotropic effects on male fertility. By extrapolation, we estimate that there are at least 40 such loci on the *X* chromosome alone, and more than 200 across the entire genome. Because these species exhibit little DNA-sequence divergence at arbitrarily-chosen loci (many polymorphisms are shared), it does not seem likely that the extensive functional divergence we have observed could be due mainly to random genetic drift. We hypothesize that adaptive fixations with pleiotropic effects on male fertility account for the discrepancies between DNA-sequence and functional analyses. Strong epistatic interactions between conspecific genes in a hybrid background appear to be the rule for hybrid sterility between recently-diverged species of *Drosophila*. These conclusions favor Sewall Wright's belief in the ubiquity of gene interactions, pleiotropy, and the complexity of the relationship between genotype and phenotype.

Moose, *Alces alces*, lacks microsatellite variation within and between Eurasian and Canadian populations

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We have investigated microsatellite variation in Finnish, Siberian and Canadian moose belonging to four different subspecies (*A. a. alces*, *A. a. pfizenmayerii*, *A. a. cameloides* and *A. a. andersoni*). Variation at six loci was studied in each geographical area from 4-20 unrelated individuals. Four of the primer pairs used (HEL10, HEL12, HEL14 and HEL40) were originally designed for bovine ms-variation study. These primers revealed extremely low variation in moose, both within and between the geographical areas. Three of the loci were monomorphic and only one from the 37 moose individuals screened for variation at HEL12 locus turned out to be heterozygous. In order to uncover hidden variation the sequences for the most common allele at HEL12 and the only allele perceived at HEL14 locus were determined for each population. The only difference found was one TA-repeat more in the compound type ms-stretch of HEL12-locus in the Canadian population. In cattle and sheep these primers have revealed high heterozygosity and a large number of alleles. A preliminary search of microsatellites from the genome of moose suggests lower frequency of these loci than in *Bovidae*. Further, moose microsatellites seem to be generally very short. The longest found were (AC)₁₁ and (AC)₇. Primers were designed to these two loci, which proved monomorphic, too.

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Social insect populations have a hierarchical structure, populations consist of more or less sedentary colonies formed by both reproductive and non-reproductive individuals. Sexual individuals have a short period when they disperse, followed by a long sedentary phase - the life-span of an individual ant queen can well exceed 20 years. Dispersal and gene flow are connected to modes of colony foundation. New females can join the natal colony without dispersing at all, new nests can be founded in the close proximity of the natal nest by splitting, or females can fly off and establish new colonies elsewhere. Males are commonly expected to disperse in all these cases.

Adding new daughters to existing colonies leads to positive genetic relatedness of coexisting reproductive females. The expected relatedness should equal the inverse of the number of females in a nest. This is roughly supported by genetic data. A social structure with many reproductive females in a nest and colonies with interconnected nests established by budding, promotes possibilities for geographic genetic differentiation. Comparison of intraspecific populations or closely related species with different social structures, shows that genetic differentiation (measured by F_{ST}) is an order of magnitude larger among populations with multi-queened colonial networks than among populations with single-queened territorial colonies.

Restricted dispersal of females affects the optimal resource allocation of colonies in two ways. Local resource competition between related females should lead to male-biased sex ratios. When the colonies adopt new females, a part of the worker force should be counted as sexual investment supporting reproduction by these females. As a result, the sex ratio among the sexual individuals becomes male-biased. The investment in males depends on the parameter defined as the fraction of gene pool contributed by the dispersing females. As predicted, sex ratios in ants forming multi-queened colonial networks are commonly highly male-biased. The dispersal model gives also predictions that can be used to test the queen-worker conflict over sex allocation. There are too little data on dispersal to test the predictions.

PHYLOGENETIC RELATIONSHIPS IN THE GENUS LIMONIUM
(PLUMBAGINACEAE) INFERRED FROM cpDNA RESTRICTION ANALYSIS.

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The genus *Limonium* (Plumbaginaceae) is very rich in rare, endemic and endangered species in the Spanish Mediterranean coast. These features are mainly due to their genetic system - this genus is rich in polyploid species, including many triploids- and to their reproductive system - with a large number of apomictic species. In addition, there is ample evidence that hybridization has played a major role in speciation in this genus, with several species having being described as hybrids between morphologically similar putative ancestors. For others, a hybrid origin has been postulated but there is no knowledge on the possible ancestors. In order to resolve this complex phylogenetic history we have started a molecular phylogenetic study of which we present our first results using restriction analysis on chloroplast DNA of several species of the section *Limonium*.

Sperm competition games

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Sperm competition appears to have been a major force in evolution. I shall outline some game theory models which predict the allocation of sperm number and size under different behavioural circumstances.

**FEMALE PREFERENCES FOR MALE DRUMMING SIGNALS IN
A WOLF SPIDER *HYGROLYCOSA RUBROFASCIATA***

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Sexual display in *Hygrolycosa rubrofasciata* wolf spider is characterised by the drumming behaviour of courting males. Males move around the habitat and produce drumming voices by percussing dry leaves with their abdomen. When females are willing to copulate they respond to male courtship by shaking their body vigorously thereby producing a weak drumming. It has been found that females prefer males that are drumming most actively. In addition the drumming of the most preferred males is more intense in the amount of hits per single drumming.

To study the female choice behaviour and the essential elements of male courting signals I investigated the activity and rate of female response for playbacks of manipulated male signals. The manipulated components of the signals were frequency (drumming bouts per time), volume, and intensity (number of strikes in one drumming bout) of drumming. Manipulation of volume level was introduced to study the search costs females are ready to face in order to choose between males.

Results of this experiment indicate that female *H. rubrofasciata* prefer male signals played with greater frequency and intensity level. Male drumming activity has previously been shown to correlate with male viability indicating that male drumming activity and intensity of drumming may be an indicator of male physical condition and quality. Thus, by choosing more actively drumming males females might be able to get better quality mates. Results of search cost level manipulation indicate that females are not ready to pay any high searching cost to choose between males. However, because males are searching and courting females actively and male quality is correlated with courting activity, females might easily achieve good quality males as mates.

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Karyotype evolution and genome size in muricid gastropods.

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The Muricidae is a widely-distributed family of carnivorous marine snails inhabiting the littoral or sub-littoral zones of rocky shores. In all but one of the muricid species which have been examined karyologically to date, diploid chromosome number is in the range $2n = 60 - 70$. However, the Atlantic dog-whelk, *Nucella lapillus*, has undergone a marked reduction in chromosome number since its ancestral form dispersed into the north Atlantic from the NE Pacific, via an Arctic route, during a period of global warming, < 5 MYA. *N. lapillus* is also unusual in having a Robertsonian polymorphism affecting 5 pairs of metacentric chromosomes in the $2n = 26$ form (diploid range = $26 - 36$), which has its centre on English Channel coasts, where chromosome number correlates with the degree of wave action on the shore. In this study we have compared the genome size of 8 muricid species from the N. Atlantic and NE. Pacific (*Nucella lapillus*, *N. canaliculata*, *N. emarginata*, *N. lamellosa*, *Ocenebra erinacea*, *Murex brandaris*, *M. trunculus*, *Thais haemostoma*) to determine whether the reduction in chromosome number in *N. lapillus* has been accompanied by a reduction in nuclear DNA content compared to the congeners in the Pacific and the other members of its family.

Chromosomes of *Ocenebra erinacea* and *Thais haemastoma* ($2n=70$) are predominantly sub-metacentric and sub-telocentric, and are $2\mu\text{m}$ to $7\mu\text{m}$ in length, whereas those of *N. lapillus* ($2n=26$) are mainly metacentric with lengths of $2\mu\text{m}$ to $10\mu\text{m}$. Karyotypes of the Pacific *Nucella* species have yet to be examined, but they are all reported to have 70 chromosomes. Total diploid length for the $2n=70$ species was approximately twice that of *N. lapillus*, but genome size, as measured by Feulgen densitometry, was either slightly less or the same as *N. lapillus*. These results indicate that genome-size reduction or polyploidy have not played any part in the evolution of this group of gastropod molluscs, and do not explain the marked reduction in chromosome numbers in *N. lapillus* which appears to have occurred following its establishment in the Atlantic since the Pliocene.

Diagnosis of Sibling Species of *Drosophila* by Three Molecular Techniques

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D.subobscura has recently colonized the west coast of North-America and presents a north-south cline: the species is very abundant in the north of California, Oregon and Washington, and gradually decreases until it disappears in Southern California. Colonization success could depend on the possible competition between the colonizing species and the nearctic species of the *obscura* group coexisting in the colonized area. According to previous studies, among the nearctic *obscura* group, the distribution range of the sibling species of the *affinis* subgroup: *D.azteca* and *D.athabasca* do not overlap. A significant increase in the abundance of *D.subobscura* is found in Northern California and Southern Oregon, an area in which no data on the *affinis* subgroup species are available. This would suggest a possible influence of these species on the colonization process. Isofemale lines of *D.azteca* from Gilroy and of *D.athabasca* from Seattle have been characterized using three molecular techniques: allozyme electrophoresis (12 loci), mtDNA (11 restriction enzymes) and random amplified polymorphic DNA (RAPD) (20 primers). All three techniques allow us to differentiate between the two species although the interspecies variation is higher for RAPDs (85%) than for mtDNA (45%) and allozymes (42%). Four localities from Northern California and Southern Oregon were sampled; in Fort Bragg (CA), Crescent City (CA) and Medford (OR) only *D.azteca* was found, while in Eureka (CA) only *D.athabasca* was detected. No conclusive explanation can be drawn from these data unless more samples within the contact zone of *D.athabasca* and *D.azteca* are analyzed.

**Lack of Recombination between Chromosomal Arrangements in
*Drosophila subobscura***

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D. subobscura is a species with a rich chromosomal polymorphism. This phenomenon prevents the recombination of genes located in the inversions or in its neighbourhood. Further, the recombination between many chromosomal inversions is also absent. The recombination in heterozygotes of the karyotype $O_{3+4+7+8}/O_{3+4}$ has been analyzed in order to understand the origin of this complex and infrequent arrangement. No recombinants have been observed out of 415 chromosomes analyzed. The recombination between the O_3 inversion, associated with a lethal gene in the American colonizing populations, and the O_{3+4} arrangement has also been analyzed in heterozygotes. No recombinants were detected among 437 chromosomes analyzed, but an interesting segregation distortion was observed, the O_3 being more abundant in the offspring (59.95%).

Preliminary analysis of satellite-DNA in four species of Tapetinae (Bivalvia Veneridae).

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Phylogenetic studies on molluscs are usually based on morphological analyses of shell, radula and genital apparatus. The need of phylogenetic analyses based on new approaches is increasingly felt. Populations of four taxa of the family Veneridae, subfamily Tapetinae, (Mollusca Bivalvia) were analyzed: "*philippinarum*" Adams & Reeve, 1850, "*decussatus*" Linné, 1758, "*aurea*" Gmelin, 1791 and "*undulata*" Born, 1780 variably ascribed to *Tapes* Von Muehlfeldt, 1811, *Paphia* Roeding, 1798 and *Venerupis* Lamarck, 1818. These genera are the most representative of the subfamily. The taxa "*philippinarum*" and "*decussatus*" are solidly ascribed to *Tapes*, for their shell surface sculpturing, while "*aurea*", usually ascribed to *Venerupis*, a genus characterized by smooth shells, has been recently assigned to *Paphia*, on pallial sinus features. On the other hand, the pacific "*undulata*" is a typical *Paphia*, which can be taken as a reference taxon. Allozymic analysis of 12 populations of the four species revealed a clear inconsistency with morphological data: "*philippinarum*" samples show a lower Nei's genetic distance D, when compared to "*aurea*" rather than to its congeneric "*decussatus*". On the other hand, "*undulata*" sample shows an intermediate level of differentiation, in spite of its conchological features, suggesting a closer similarity to the "*philippinarum*" - "*aurea*" cluster; *T. decussatus* appears the most differentiated among analyzed species (Passamonti et al., submitted). A preliminary analysis on genomic DNA with several restriction endonucleases (7-23) was undertaken to find out highly repeated fractions. The analysis showed the presence of a multimeric ladder in the "*philippinarum*", "*aurea*" and "*undulata*" digests with Bgl II, Hae III and Alu I endonucleases. No visible multimeric ladder was found in "*decussatus*" digests. Southern blot hybridization utilizing the monomer cloned in "*philippinarum*" (phiBgl II -420pb) showed a higher affinity of the DIG-labeled probe with "*aurea*" digests than with "*undulata*" ones. These sequences are absent from "*decussatus*" DNA, since no hybridization signal was observed. Although preliminary, these hybridization patterns confirm the "*philippinarum*" - "*aurea*" genetic affinity and support the hypothesis that "*decussatus*" could be the most differentiated taxon of the group. In conclusion, Southern blot hybridizations fully parallel electrophoretic data and clearly indicate an inconsistency between morphological and molecular taxonomy of the four species.

Passamonti M., Mantovani B. and Scali V. Allozymic Characterization and Genetic Relationships among Four Species of Tapetinae (Bivalvia Veneridae). Submitted.

On the evolutionary stability of onthogenesis in a state dependent
model of Leslie type for population with age structure

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Selection pressure is not limited by influence on qualitatively changing discrete or continuously varying metric traits. More complex objects such as, for example, curves of trait onthogenetic development are also subjects of its operation. Consider a population with overlapping generations which dynamics obeys Leslie matrix population model with demographic coefficients depending on some parameters. Let the vector of parameters can be partitioned on subsets of the same size and each of them influences on demographic characteristics of only one age class. We interpret these subsets as values of some traits of individuals at appropriate age. Then the ordering of the considered subsets by age gives a picture of an onthogenesis of traits. To study a problem of onthogenesis evolutionary stability, a model of competition of the given type populations is introduced. Birth and death coefficients of populations are allowed to be dependent on the whole state of the competition community. Linear stability analysis of its monomorphic equilibria shows that net reproductive rate of the stable resident population exceeds corresponding rates of invaders. Let functional expressions for birth and death coefficients of populations be the same, and populations differ in parameter values (development trajectories). Then the evolutionary stable trajectory gives a maximum to the function of net reproduction rate, i.e. the offspring number of individual produced during life cycle. If the number of age classes is great and the age differences between them are small, we may approximate the sum of produced offsprings in the net reproductive rate by integral and receive that evolutionary stable (infinite-dimensional) onthogenesis is a solution of a variational problem: it gives a maximum to the functional of net reproductive rate. That is, searching for an evolutionary stable onthogenesis reduces to solution to some variational problem.

GENETIC VARIETY AND PHYLOGENY OF THE ANSERIFORMES ORDER

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For many groups of free-living organisms, biochemical and molecular approaches are now standard methods for reconstructing evolutionary history and characterized at population level. We investigated genetically determined protein variability of blood serum and other biological liquids of Anseriformes order water fowl and their phylogeny. The material was obtained during expeditions in different locations of Polyarctics, Far East, Kazakhstan of the former USSR and in Lithuania. Total number of the water fowl species investigated was 26 including 17 species of the Anatinae, 5 species of the Anserinae, 4 breeds of the domestic geese and 1 breed of the domestic ducks.

Comprehensive phylogenetic data obtained by methods of morphophysiological are given Johnsgard (1978). Dendrogram of the Anseriformes order which we submitted has been calculated based on cluster analysis of the genetic distances (by Nei and Roger) and the method of UPGMA.

Our dendrogram reflects possible way of phylogenies in *Anas* genus. The data of this dendrogram shows that mallard ducks and *A. querquedula* which habitat in a common area and have similar way of life, are genetically closed. Genetic difference composed only 0,467. Meanwhile the difference in mallard ducks and other species of *Anas* genus is much greater. The results of our investigations confirms that mallard ducks and *A. querquedula* have the greatest quantity of common morphs, when with other species from *Anas* genus.

The tribes Mergini and Anserini are the most remote according to electrophoretic data of genetic variety in proteins. Above tribes in the course of evolution have earlier separated from common ancestor than other investigated tribes. Sea ducks, merganser and eider ducks which have common ancestors cover separate branches in the phylogenetic tree. Above species are closer to the diving ducks than to the river ducks according to genetic data. The Cairini tribe which covers a separate branch in the phylogenetic tree of the Anseriformes has common ancestors with river ducks, but differs considerable from other birds of the geese order according to morphophysiological data and the way of life. This expressed difference from tribes of Anserini, Anatini, Somaterini is confirmed by our presented investigation data of genetic variety.

Genetical relatedness in a communal bee using microsatellite loci.

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The existence of eusocial insects has for long intrigued evolutionary biologists because of the altruism that workers within such societies exhibit. Kin selection has been invoked to account for the evolution of eusociality, and helps to explain why sociality has evolved most frequently in the haplodiploid Hymenoptera; full sisters within a haplodiploid species are more closely related than those within a diploid species, relaxing conditions under which altruism is favoured. Relatedness thus becomes a central element to the understanding of sociality. Paradoxically coefficients of relatedness within nests of eusocial ants, bees and wasps are often low, but may reflect other selective pressures operating within eusocial societies.

To understand better the role that kin selection may play in favouring the evolution of sociality we have measured genetical relatedness in a facultatively communal bee, *Andrena jacobi*, using microsatellite markers. Communal species are considered to have one of the lowest levels of insect social organization. Within *A. jacobi*, for example, between 1 to 600 females share a common nest entrance in which they provision offspring, yet within the nest each female provisions her own offspring without help from others.

Microsatellite markers proved to be highly variable. Intranidial relatedness estimates did not differ significantly from zero for 3 of 4 loci (range of relatedness values: +0.07 to 0.00). There was no significant relationship between intranidial relatedness and the number of females sharing a nest entrance. Kin selection therefore seems to have little or no role in favouring the existence of communal behaviour in *A. jacobi*. These results concur with allozyme and DNA fingerprint studies of other communal bee species. They also support the view that communality may be a stable level of sociality, not a transient bridge between solitary and higher levels of social organization.

Effectively neutral alleles have associated selection coefficients in the range $-1/2N_e < s < 1/2N_e$, where N_e is effectively population size. As a result of these relatively small selection coefficients, effectively neutral alleles can drift up to high frequencies, just like perfectly neutral alleles (for which $s=0$). In this talk, we present the results of a computer simulation study that used a multi-locus mutation scheme which was inspired by the ideas of R. A. Fisher. The scheme allows for both beneficial and deleterious mutations. Furthermore, mutations can be of any magnitude.

We consider average fitness after a stationary distribution has been achieved. The results show that mean fitness declines as the proportion of asexually-produced offspring becomes larger. This effect can compensate for the cost of sex and lead to the success of obligately sexual species in ecological competitions against asexual or partially-asexual species. An intuitive explanation of the results is provided, and data on the effects of sex on the distribution of selection coefficients is presented. We also show that asexuality can greatly reduce the rate of adaptation after an environmental change. Finally, we present data on the rate of decay in fitness after a population has undergone a transition from sexuality to asexuality, and we discuss the importance of this data for understanding within-species competitions between obligately sex and asexuality.

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Phylogenetics of tropical trees: combining molecular and morphological data in *Andira* (Leguminosae, Dalbergieae) to study dispersal biology

Andira comprises approximately 30 species of trees and shrubs distributed throughout the neotropics, with one species reaching Africa. It has unusual, drupaceous fruits that are either small, and dispersed by bats, or large, and probably dispersed by large rodents. Cladistics is becoming a preferred method for generating phylogenetic hypotheses, but the majority of morphological characters in *Andira* are not suitable for cladistic analysis because they display continuous variation and cannot be objectively subdivided into character states. This lack of characters results in an unresolved morphological cladistic analysis for *Andira* species. In contrast, an analysis of chloroplast DNA restriction site variation resolves relationships among groups of species, but fails to resolve relationships within these groups. Direct combination of all molecular and morphological characters in a single cladistic analysis provides the strongest and most resolved phylogenetic hypothesis. This hypothesis suggests that previous infrageneric classifications require revision, and is consistent with recent, rapid speciation in eastern Brazil. It demonstrates multiple, independent origins of large, rodent dispersed fruits from small, bat dispersed fruits. Patterns of morphological variation in *Andira* are typical of speciose genera of woody, tropical plants, and this example demonstrates that combined cladistic analysis of molecular and morphological data may provide a useful approach for phylogenetics of these organisms, which are an important component of diversity in tropical vegetation.

Life-history responses to predation in *Physa acuta* (Gastropoda)

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Life-history theory predicts that an organism's resource allocation patterns should depend on extrinsic mortality factors. Adaptive response to changes in mortality regime may arise through either genetic evolution or phenotypic plasticity.

To investigate these topics, I subjected experimental populations of the freshwater snail *Physa acuta* to different mortality patterns. Besides controls (no predators) some populations were subjected to predation by one of two species of predatory flatworms that were found to show strong size-dependences in their predation.

One predator (*Macrostomum* sp) feeds only on small juveniles (up to 2 mm). Theory in this case predicts a shift in prey life-history towards larger offspring. The other predator (*Dugesia polychroa*) feeds on adult snails as well, but only up to 6-7 mm. In this case, theory predicts shifts towards both larger offspring and larger adults.

These precise shifts were observed in the experimental populations within 3 months of coexistence with predators. *Macrostomum* presence induced a shift towards larger eggs, but did not affect *Physa* adult size. By contrast *Dugesia* induced shifts towards both larger adults and larger eggs.

Since some of these responses to predation might be indirect (e.g. mediated by changes in snail density and/or biomass) I performed analyses of partial effects as well as density-manipulation experiments. Predator presence remained the most significant factor responsible for the observed shifts. I conclude that *Physa acuta* can adjust on a plastic basis important life-history traits to the presence of different types of predators.

THE SPREAD OF AN ADVANTAGEOUS ALLELE ACROSS A BARRIER:
EFFECT OF DEME SIZE AND SELECTION AGAINST HETEROZYGOTES.

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Tension zones could be viewed as genetic barriers to gene flow. If a cline is associated with a physical barrier, as has been documented for many chromosomal races, the effect on gene flow should be substantially increased. Cline theory predicts that even a mildly advantageous allele can easily penetrate past a barrier with the rate of spread affected by population density. How will the spread be affected when these factors act at the same time?

We have investigated the relationship between time to fixation of an advantageous allele and its delay as a function of increasing physical barrier, selection against heterozygotes and deme size. A Monte-Carlo simulation based on a 2-dimensional stepping-stone model with an array of 8x20 demes was used. Time to fixation is defined here as time in generations spanned from the initial contact between two races to the point when the advantageous allele has reached fixation.

The following trends have been observed:

1. No selection against heterozygotes
 - (i) the advantageous allele is hardly affected by a physical barrier
 - (ii) increasing deme size tends to shorten the time to fixation.
2. Selection against heterozygotes
 - (i) for low values of selection against heterozygotes and weak physical barrier the spread of advantageous allele is faster when demes are larger
 - (ii) with increasing selection against heterozygotes and/or physical barrier the opposite trend is observed: time to fixation is lower when deme size is small
 - (iii) genetic drift contributes substantially to the probability of crossing both genetic and physical barriers.

284 *WOLBACHIA* INFECTION IN *DROSOPHILA SIMULANS*: T14 DOES THE BACTERIA MODIFY THE FITNESS OF ITS HOST ?

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Wolbachia are endocellular bacteria of arthropods, transmitted only through the cytoplasm of the egg. In *Drosophila simulans* they can be responsible of cytoplasmic incompatibility, a high embryonic mortality when infected males are crossed with uninfected females. This phenomenon gives an advantage to the infected cytoplasm, allowing the infection to spread in the population. The question asked is whether bearing the endosymbiont involves a cost to the infected female. The fitness effect of two bacteria, *wHa* and *wNo*, has been studied in three different cytoplasmic combinations (one bi-infection and two mono infections). The fitness of infected *Drosophila simulans* strains has been compared to that of replicates cured from their bacteria following an antibiotic treatment (tetracycline). Only uninfected males were used in the experiments to exclude cytoplasmic incompatibility. The components of fitness studied were development time, fecundity, hatch rate, egg-to-adult survival and number of offspring (productivity). No significant differences were found in development time, hatch rate and egg-to-adult survival. A lower productivity in tetracycline-treated strains was detected three generations after treatment in all strains. This lower productivity was still present five generations after treatment in the replicate cured from its *wNo Wolbachia*. A last experiment carried out 14 generations after treatment failed to reveal any difference in productivity in this strain between infected and uninfected replicates. At this time, further experiments involving all three cytoplasmic combinations did not reveal any difference in fecundity between infected and uninfected replicates. The results are discussed in terms of selective pressures bearing either on the *Wolbachia* or on their host. Our results support the idea that parasites transmitted exclusively through the egg will tend not to harm their host.

Key words: *Wolbachia*, *Drosophila simulans*, endosymbiosis, fitness, cytoplasmic incompatibility.

Behavioural changes in Ruddy Shelducks (*Tadorna ferruginea* Pall.) of the Askania-Nova population

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A.B. Popovkina (Moscow State University, Russia) T8.

Ethological studies were carried out in the Askania-Nova Nature Reserve (Ukraine) from 1987 till present. No Ruddy Shelducks inhabited this region until the end of the last century. The first attempts to introduce them there were made in 1886, when 16 young birds were released in the Reserve. In 1889 the first nesting was recorded. Since then, the population greatly increased. Now the water bodies of the Reserve house a unique population of free-living Ruddy Shelducks; their number exceeds 600 in the summer period. The birds are supplied by food all year round; in addition, there are many natural (tree holes and burrows) and artificial (wooden boxes) nesting sites. This attracts birds and promotes extremely high population density. It is maintained by specific behavioural mechanisms. In nature, Ruddy Shelducks exhibit high territoriality and aggressiveness. A pair of these birds is known to protect an area of more than 1 sq.km in the natural habitats. In Askania-Nova, up to 60 pairs have been nesting in the recent years on the territory less than 20 ha. Most of them nest on small islands 10 to 50 m long. The nests may be located 7 to 10 m apart. Double and triple clutches, as well as joint clutches with mallards and other ducks are frequent. (This phenomenon is also observed in nature, though very rarely). After the young hatch, up to 5 broods may occupy a pond of 5.6 ha. Due to the low level of aggression, many cases of brood amalgamation were observed. (No "creches" of the Ruddy Shelduck in nature, contrary to the Common Shelduck (*Tadorna tadorna*), are known to the author). Aggression of the Ruddy Shelducks towards conspecifics is usually expressed in more ritualized form than in the wild. Meanwhile, they sometimes would show aggression towards unusual objects. Since 1955, the resident birds remained in Askania-Nova for winter; now more than 200 individuals winter in the Reserve. Such deep long-term changes in behavior provide the existence of the unique population of *Tadorna ferruginea* in Askania-Nova Nature Reserve.

EVOLUTION OF MAJOR SPERM PROTEIN GENES IN PARASITIC AND
OTHER NEMATODES

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Major Sperm Protein is unique to nematodes and coded by a small gene with two exons. Known copy number varies from one to 50, with pseudogenes, depending upon species. In Filarial parasites there are around five copies with a rate of concerted evolution by non-homologous recombination slower than the rate of speciation. As a result different parts of the same gene at the same locus can show a different evolutionary history and are not suitable for recovering the species-phylogeny. This pattern of evolution may be shared with repetitive genes for some structural proteins in other taxonomic groups. The single intron is not present in all species of nematode and appears to have been lost. In some species the intron seems to show sequence homology with mariner.

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Selection against hatchery genes in brown trout experiment

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Hybridization is widespread in fish, especially in freshwater species as Salmonids (Schwart, 1981). Their ability to hybridize can be explained by external fertilization and weakness of the reproductive barriers, due to the recent differentiation between Salmonids species (the quaternary period). Human transfer of hatchery stock into rivers inhabited by congeneric populations correspond to a secondary contact. In brown trout (*Salmo trutta fario*), the degree of divergence between Mediterranean and Atlantic populations is of the same order as one found in Salmonids subspecies in North America (Fouldenslager and Gall, 1980). Unsuccess of restocking in the Mediterranean drainages can be due to environmental factors, but recent results of native populations analysis argue for a selection against hatchery genes (Poteaux *et al.*, submitted). In order to demonstrate it, a backcross experiment was conducted. Three diagnostic allozymic loci and four microsatellite loci were analysed on two sets of 160 individuals. No counter-selection evidences were obtained except on one allozymic locus in one set.

Key-words : brown trout - *Salmo trutta fario* - backcross experiments - alozymes - microsatellites - counter-selection

Phylogenetics relationships and systematic on the *Oreochromis niloticus* subspecies-complex (Pisces: Cichlidae) with use of microsatellites markers.

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The African cichlid *Oreochromis niloticus* (Linnaeus) is one of the most important fishes in tropical fresh-water aquaculture. Seven subspecies have been described on morphological characters by Trewavas (1983).

Many authors tried to study relationships among these subspecies with difficulty, as no completely diagnostic characters exist. Seyoum *et al.*, (1991) investigated the sub-species complex using restriction endonuclease analysis of mitochondrial DNA. Changes in nomenclature were proposed, 1 subspecies renamed (*Oreochromis niloticus filoa* as *O. ancellatus filoa*) and 1 species created *O. niloticus tana*. Nevertheless, these study couldn't reveal sufficient differentiation between the other subspecies.

Our study presents the genetic polymorphism of 5 microsatellites loci. These loci were obtained from a partial genomic bank of an other African cichlid *Sarotherodon melanotheron* Rüppell, 1852).

These results show clear differentiation between each sub-species. Diagnostic alleles are presented. Phylogeographic relationships and biogeographic scenarios are proposed which increase our understanding of speciation events in this complex.

Contrarily to a widespread opinion, our study clearly shows that moderately polymorphic microsatellite loci such as those we have worked out for tilapiines species (3 to 7 alleles / loci) are excellent phylogenetic markers.

A review of the chromosomes of *Corydoras* catfishes, with a preliminary report on *C. adolfoi* and *C. imitator*, sympatric species from a tributary of the Upper Rio Negro.

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T12

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The genus *Corydoras* Lacepede is placed within the Callichthyidae, one of almost twenty families in the order Siluriformes that are commonly known as catfishes. There are eight callichthyid genera, which are all characterised by the possession of two lateral rows of scutes or bony-like body plates. All callichthyid catfish are small, primarily freshwater species. There are about 130 *Corydoras* species known to inhabit small streams and running pools throughout tropical South America.

Many species can be identified from their distinctive but simple monochromatic patterns made up of black spots, lines or stripes on tan or pale white body colours. The patterns are considered diagnostic and of taxonomic value by many authors. However, pigmentation patterns are known to be often variable both within and among populations, and there have been no comprehensive studies of geographic variation in even a single species. Additionally, there is a high occurrence of sympatric, morphologically distinct, pairs or groups in the genus. For example, *C. adolfoi* and *C. imitator* are sympatric in tributaries of the Rio Miua, part of the Upper Rio Negro system in Brazil. They share a remarkably similar pigment pattern, and some authors originally questioned whether or not they were distinct species. *Corydoras* are also known to exhibit some of the highest variation in DNA levels and karyotypes known among fishes. Nuclear DNA content has been reported to vary between 1.04 and 8.75 pg/nucleus and diploid chromosome number between approximately 40 and 132.

The genus therefore offers the opportunity to study the possible role of sympatric speciation and polyploidy in the evolution of *Corydoras*. In this paper, previous work on the genome of *Corydoras* is reviewed, and preliminary results are presented on the chromosomes and DNA content of *C. adolfoi* and *C. imitator*.

Levels of DNA sequence variation in a *Drosophila melanogaster* pseudogene provide evidence of linked directional selection.

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and

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It is expected on theoretical grounds that if directional selection is a frequent player in evolutionary processes, then one should observe reduced levels of variation in regions of low recombination. There is some evidence that this is the case in *Drosophila*. The question addressed in this study is whether this so-called "hitchhiking effect" can be strong enough to maintain low levels of variation at a completely unconstrained locus. We have examined within-species DNA sequence variation in a *D. melanogaster* cuticle protein pseudogene (*LCP Ψ*) which lies in a region of infrequent recombination. The observed level of variation is much lower than at many other *D. melanogaster* loci. This contrasts sharply with phylogenetic evidence showing a high substitution rate in the pseudogene. These data are used to infer that strong or frequent directional selection has occurred in the recent evolutionary past in the region containing this gene.

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The genetic structure of twelve populations of *Pinus mugo* from Tatra Mts. growing on limestone, granite and peat bogs were studied by means of isoenzyme electrophoresis.

These three groups of populations differ in several genetic parameters. Populations from the limestone are most heterozygotic, possess in average more alleles and genotypes per locus. Those from the peat bogs are less heterozygotic and showing lower number of alleles and genotypes. The populations from the granite are intermediate as far as investigating genetic parameters are concerned.

All populations are close to Hardy-Weinberg equilibrium. The G_{ST} coefficients indicate the higher differentiation of the populations from the peat bogs than from the limestone or the granite. There is no correlation between the geographic origin of populations and the genetic similarity according to Nei's and Hedrick's formula.

The multilocus analysis of single samples reveal the significant level of vegetative propagation in the populations of this pine species.

Relationship between incidence and amount of migratory activity in the blackcap (*Sylvia atricapilla*) - Consequences for the evolution of sedentariness in a migratory bird species

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T8

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Over its entire range, the blackcap (*Sylvia atricapilla*) is highly differentiated with respect to migratory behaviour. Individuals from northern populations are long-distance migrants and 'completely migratory'; those from southern populations are partially migratory and migrate only short distances. Blackcaps from some Atlantic islands do not migrate at all. In previous experiments it has been shown that different components of migratory behaviour in this species are to a large extent genetically controlled.

Drawing on data for migratory restlessness of almost 1000 blackcaps from different partially migratory populations, we studied whether the amount (a continuous trait) and the incidence (a dimorphic trait) of migratory activity are inherited as one or two distinct traits. We predicted that if incidence and amount were only one trait, the distribution of migratory activities in each population should be accurately described by a censored normal distribution. We developed a simple method for estimating means and variances from the empirical data and used these estimates for computing realized heritabilities. In all populations the censored normal distribution gave a very good fit to the actual distribution of migratory activities in the parental generation (= in the wild). These findings and the results obtained from the comparison of resemblances among family members, including or excluding individuals with zero activity, strongly suggest that incidence and amount of migratory activity is only one trait. Hence, birds with no activity are not categorically different, but at the lower end of a continuous distribution of activities. These results suggest that partial migration and sedentariness can be selected from a completely migratory population within few generations.

A multilocus model of the selection barrier between populations

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One of the postzygotic mechanisms that may contribute to the formation of isolating barriers between populations may be selection against the introgression of genetic material from one to another population. To quantify the selection barrier between separate populations that evolve in different environments Zhivotovsky and Christiansen (Evolution, in press) have introduced the strength of the selection barrier as the eventual survival of the descendants of a small group of immigrants from a donor population with respect to the survival of individuals of the recipient population, and analysed the case of genetically closed populations. We generalize this model for the arbitrary distance between populations subject to weak viability selection on multiple loci, and calculate the strength of the selection barrier in terms of the initial differences in allele frequencies and linkage disequilibria between the populations. The special case of stabilizing selection on a quantitative trait is considered, in which the strength of the selection barrier is represented in terms of variance components.

RELATIONSHIPS BETWEEN GENOMIC CONFLICT AND PHENOTYPIC INSTABILITY FOLLOWING SYMPATRIC AND ALLOPATRIC MATINGS IN BASIDIOMYCETE FUNGI

IT 9

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Following mating in the basidiomycetous fungi, populations of nuclei and organelles are brought together that are capable of forming diverse and unstable relationships. Genomic disparity arising within a cell, either in a *genetic* sense (as a result of non-self fusions), or an *epigenetic* sense (as a result of self-fusions between cells in alternative developmental states) engenders the possibility for conflict, coercion and/or confusion at the cellular level. According to circumstance this may also lead to complexity and instability at subsequent developmental, population biological and evolutionary scales of organization.

These possibilities have been examined in the context of naturally-occurring and laboratory synthesized heterokaryons of two fungi producing mycelia with multinucleate hyphal compartments, *Heterobasidion annosum* and *Stereum hirsutum*. Using a combination of fluorescence light microscopy, molecular DNA fingerprinting techniques and laboratory-based pairing experiments, nuclear and mitochondrial genomes have been followed through a variety of sib-related, non-sib-related sympatric and non-sib-related allopatric heterokaryotic associations.

Patterns of genomic exchange were examined during heterokaryon formation. In addition, observations on the allocation of nuclei to hyphae and conidia, the somato-sexual responses of homokaryons recovered from heterokaryons via conidia (compared with their progenitor basidiospore-derived counterparts); and the influence of different genomic combinations upon spore germinability and post-germination mortality were also investigated. The patterns observed were strongly supportive of the occurrence of intracellular genomic conflict, particularly in the non-sib-related sympatric and non-sib-related allopatric associations. Differences in the behaviour of laboratory synthesized heterokaryons and naturally-occurring heterokaryons suggest that genomic conflict may act as a strong selective force in natural populations, effectively removing maladapted heterokaryotic associations from a population. Furthermore, in sympatric populations, co-evolutionary feedback processes may operate to reinforce those mechanisms that prevent or limit the take-over of genomic territory by non-self genetic entities.

The possible interpretation of these findings in terms of genomic conflict will be discussed, along with a consideration of the options available to fungal systems for the attenuation of such conflict.

Evolutionary dynamics of some spatially-extended individual-based models.

D. A. Rand

I will discuss dynamics and evolution in spatially-extended individual-based models. Such systems display a range of new phenomena and their behaviour can differ radically from that of mean-field models. In particular, I want to consider the evolution of transmissibility and virulence in host-parasite systems and a spatial mechanism for the evolution and maintenance of sexual reproduction.

In the former there a range of new dynamical and evolutionary phenomena. In particular, (i) in this system selective pressure is substantially reduced compared to the corresponding mean-field models and artificial suppression of the pathogen population leads to faster evolution and reduces evolutionary stability; (ii) unlike the mean-field models, there exists a critical transmissibility T_c above which the pathogen dies out and (iii) the system displays *self-evolved criticality*. If the transmissibility T is allowed to mutate, it evolves to the critical value T_c . Thus the system evolves so as to put itself at the boundary of where it can exist.

For the latter I will present a spatial mechanism by which sex can resist parasites by creating genetic diversity. Recombination in the host population acts so as to produce a genetic environment that, although spatially correlated, is randomly distributed in space. The propagation and evolution of parasites in such a random environment is greatly constrained and the effect is usually sufficient to overcome the two-fold disadvantage of sex. I will consider a range of models illustrating this phenomenon.

An evolutionary explanation for (IT 6) human handedness 295

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Around 10-13% of humans are lefthanded, in probably all ethnic groups. This percentage has apparently not evolved during historical times, and probably not greatly during the neolithic or at least the upper paleolithic period. Predominance of right-handed individuals is detected in the *Homo* lineage as far as 1.9 million years ago, but not in the closest living human relative (*Pan sp.*). As left-handedness is repeatedly associated with lower survival, the persistence of left-handed humans has always remained puzzling. Here we present a hypothesis for the maintenance of left-handed people, and discuss it in the context of the evolution of handedness in humans.

IS SEXUAL REPRODUCTION BY PARASITIC NEMATODES AN IMMUNE EVASION STRATEGY?

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Parasitic nematodes of higher vertebrates all have biparental sexual reproduction, whereas free-living, and parasites of plants and invertebrates frequently reproduce by selfing or parthenogenesis. One explanation for this is that sexual reproduction generates novel parasite genotypes which are less susceptible to host immune responses raised against parental genotypes. If so, parasite breeding system has clinical and epidemiological consequences; acquired immunity may also provide a selective benefit to outcrossing sufficient to offset its genetic costs.

We have been investigating this hypothesis using *Strongyloides ratti*, a nematode of rats. All parasitic adults are parthenogenetic females. Their offspring develop either into infective larvae or into free-living dioecious forms which reproduce by conventional meiosis and syngamy to produce infectious progeny. The switch between morphs is under both environmental and genetic control; artificial selection can result in the almost total loss of sexual reproduction.

If sexual reproduction is an immune evasion strategy, (i) the production of sexual morphs should be correlated with developing immunity, and (ii) host protective responses should be most effective against the genotype that elicited them. We report a variety of experiments testing these predictions.

**SKULL SIZE AND SHAPE VARIATION OF WEASELS (MUSTELA NIVALIS)
IN NORTH AMERICA**

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TIG??

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Geographic variation of weasels (Mustela nivalis) is extreme throughout its range in Eurasia and North America. The large morphological plasticity shown by the species, mainly in terms of size variation, is even more remarkable considering the high degree of ecological specialization characteristic of this small carnivore. This contrast between morphological generalization and ecological specialization has motivated numerous studies trying to find environmental interpretations (Bergman's rule, character displacement, changes of prey size) accounting for this variability. To verify those hypothesis, material from North America is particularly interesting because of the enormous diversity of habitats encompassed in its area of distribution and its sympatric and allopatric condition relative to the range of distribution of two other weasel species.

Morphological variation of this weasel species has lead to the recognition of numerous subspecies and distinct forms throughout its distribution range worldwide. A key question that needs to be answered firstly concerns the validity of those subdivisions and the taxonomic degree of differentiation between forms. Environmental hypothesis associated with weasel variability would change drastically depending on the genetic and taxonomic identity of the different forms observed (species, subspecies). This study aims towards an appraisal of the morphological variability in size and shape shown by the skull of Mustela nivalis in North America and its taxonomic and evolutionary implications. There seems to be some evidence supporting the distinctive character of the small weasel forms from North America, separating them from Eurasian taxa.

GEOMETRIC ANALYSIS OF SIZE AND SHAPE VARIATION IN BARB MORPHOTYPES FROM LAKE TANA (ETHIOPIA)

T-1

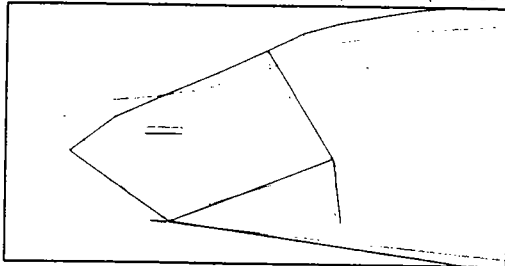
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A group of 13 distinct Barb morphotypes have been described in Lake Tana (Northern Ethiopia) and assigned to a single species Barbus intermedius, which renders this species a spectacular example of fish polymorphism. Morphological examination of size and shape variation among morphotypes was made using geometric morphometrics instead of traditional measurements, allowing the use of a more detailed information. Nineteen 2-D landmarks were digitized on each fish from photographs of 300 fresh specimens captured in Lake Tana, including 12 currently recognized morphotypes and some specimens of Varicorhinus beso, which was used as an external group. Shape analysis was mainly based on the superimposition of landmark configurations using generalized and ordinary least squares and resistant fit procedures. Results suggest that morphotype "intermedius" represents the closest form to an average type, whereas "acute" and "small eye" were the most differentiated. Morphological distances suggest the existence of two groups of morphotypes clearly defined. One group includes "acute" "barbel" "white hunch" "black hunch" "small eye" and "big eye" and the other one includes "lip" "carp" "intermedius" and "zurki". This grouping seems unrelated with size of the individuals, which was estimated by centroid size. Most differences were localized on the head and nuchal hump, which is likely to have strong functional constraints. Available data on the ecology of these morphotypes suggest ecological adaptations that parallel the morphological changes observed. Despite the key question should remain focused on the taxonomic and genetic identity of these morphotypes, a detailed account of the differentiation paths linking one morphotype to another and their functional implications will provide essential clues to understand the evolutionary history of the species in Lake Tana.



Least squares superimposition of the head region of morphotype "small eye" (dotted line) matching "intermedius" (solid line) configurations showing the spatial divergence at each 2-D landmark. Both fish configurations have been scaled to the same geometric size to allow the study of shape variation. Differences in the head shape and position of the eye and the mouth may reflect the piscivory diet of morphotype "small eye."

GENIC AND STRUCTURAL BARRIERS TO INTROGRESSION AS REVEALED BY IT4
GENOMIC MAPPING. Loren H. Rieseberg, Biology Department, Indiana University,
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199 The majority of plant and animal species that have been analyzed karyotypically differ in chromosome structure. Because certain structural rearrangements such as translocations and inversions are associated with disrupted meiosis and semisterility in interspecific hybrids, chromosomal structural differences are thought to serve as reproductive barriers between many animal and plant species. This interpretation has been questioned recently, however, because of the difficulty of distinguishing between the sterility effects of the chromosomes themselves and genic differences.

Here we describe the impact of both chromosomal structural differences and genic factors on the genomic location and frequency of introgression between two karyotypically divergent sunflower species, *Helianthus annuus* and *H. petiolaris*. Analysis of 197 mapped molecular markers in 58 backcrossed progeny between these two species revealed that 40% of the genome from seven collinear linkages introgressed, whereas only 2.4% of the genome from ten rearranged linkages was transferred. Thus, chromosomal structural differences appear to provide an effective mechanism for reducing or eliminating introgression in rearranged chromosomal segments or adjacent regions. On the other hand, observations of highly variable rates of introgression for different markers within the collinear portion of the genome suggests that genic factors also affect rates of introgression in *Helianthus*. That is, selection against *H. petiolaris* genes in concert with linkage may have reduced or eliminated parts of the genome not protected by structural changes. Co-adapted gene complexes that resist disruption could account for these results.

To test for the presence of co-adapted gene complexes, all pairs of introgressed markers were analyzed for significant associations. Two unlinked groups of markers displayed significant associations suggestive of epistasis. Both groups include markers from our linkages, indicating that gene interactions, in concert with selection and physical linkage, could greatly reduce overall nuclear gene flow. Thus, barriers to introgression among wild sunflower species include both chromosomal structural and genic factors.

300.
UNCOUPLED PATTERNS OF SIZE AND SHAPE EVOLUTION IN A FOSSIL
RODENT (*STEPHANOMYS*): A FOURIER ANALYSIS APPROACH

T1

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Size and shape evolution were investigated along the Pliocene lineages of the fossil rodent *Stephanomys*. Previous studies on this genus were mainly based on size variation and descriptive comparisons, without attempting to quantify shape changes. Hence, on the basis of regular size increase, *Stephanomys* was considered as a valuable example of phyletic gradualism. In order to quantify morphological variation within and among the lineages, a method for analysing complex outlines, the elliptic Fourier transform, was applied to tooth contour (upper and lower first molars). This allowed to compare evolution in size, estimated by tooth area, as well as evolution in shape, represented by Fourier coefficients.

While size gradually changes with time, shape gives a rather discontinuous evolutionary pattern for both upper and lower molar. The significant correlation between shape and geological time supports the existence of a global trend of morphological change through time. In terms of shape changes, fossil samples are grouped with no respect to their lineages, suggesting that the evolution of this traits occurred by steps and in a parallel way in the different lineages. These groups could thus be interpreted as stages of the morphological evolution. The correlation between upper and lower molars supports the hypothesis that this stepped evolutionary pattern may be caused by the existence of mechanical or developmental constraints rendering only few morphologies stable.

Hence such a discrepancy between size and shape evolution of a single structure suggests that these two features depends on different types of genetic determinisms and mechanical constraints, leading to different evolutionary patterns. Thus, it might be misleading to infer any evolutionary process directly either from morphological or from biometrical data.

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In this study, we describe the effects of two food sources differing in quality on life history traits of *Daphnia galeata*, *Daphnia cucullata* and their interspecific hybrid, *Daphnia cucullata***galeata*. Two clones of the three co-occurring taxa were reared on both a green algae *Scenedesmus obliquus* generally considered as a good food source, and on a filamentous cyanobacteria *Oscillatoria limnetica*. Filamentous cyanobacteria are considered as poor quality food source for zooplankton. In accordance to this, reproduction on *Oscillatoria* was generally lower than on *Scenedesmus*, but still a positive population growth rate was achieved with the exception of one hybrid clone.

A difference between the species in the way they reacted to *Oscillatoria* could be observed; *D. cucullata* seemed to be the best of the taxons at utilizing *Oscillatoria*. *Oscillatoria* had a more severe inhibition effect on *D. galeata* and the hybrid measured as the population growth rate, r . The r of *D. cucullata* did not change between the food types, thus it improved its competitive ability in relation to other species when fed *Oscillatoria*. In addition, *D. cucullata* experienced no mortality on *Oscillatoria*, in contrast to the other taxons. There was no clear difference between *D. galeata* and the hybrid in how they reacted to the food types.

There was a lot of intraspecific variation in the manner the different food types affected the growth and reproduction of the animals; a differential reaction to the two food types can especially be seen for *D. cucullata* and the hybrid clones. Both *D. galeata* clones grew and reproduced better on *Scenedesmus*. Especially in egg production there were only clonal differences and no significant differences between the species. Clearly, considerable variation in several life history traits exists between clones within these *Daphnia* taxa, especially *D. galeata* clones used. Therefore, it is important to be able to partition the within- and between species variance for different traits before making definitive conclusions about species-specific differences in such traits.

The competitive relations between the three taxons change temporally in relation to the changes in environment. According to our results, filamentous cyanobacteria in the environment improve the competitive ability of *D. cucullata*.

WHEN EXPLOSIVE CHROMOSOME DIVERGENCE DOES NOT RUN PARALLEL TO GENIC DIFFERENTIATION: THE CASE OF THE FOSSORIAL RODENTS OF THE GENUS *CTENOMYS*

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Despite its morphological uniformity, the genus *Ctenomys* shows some of the highest chromosomal variability within the fossorial species. The possible relation between chromosomal variability and high levels of genic variation has not been established in *Ctenomys*. As an attempt to clarify this latter point we have analysed, by means of allozyme electrophoresis and RFLP, 24 populations of the genus, which had been assigned to 10 different species by previous authors on the basis of morphological or cariological characteristics. Populations studied belong to the Argentinian range of the ample distribution of the genus, 7 out of the 10 species had also been previously pooled in two large groups attending to their chromosomal characteristics, coinciding with their geographical distribution, one being known as the "Corrientes group" in northern Argentina and a second one named "Mendocinus group" in the south. *Octodon degus* was used as an outgroup in the subsequent phylogenetic analysis which included all populations.

For the allozyme study a total of 38 loci encoding 19 enzymes and 2 non-enzymatic were analysed. The average genetic variability ranged from complete homozygosity ($H=0.0$) in the population of *Ctenomys roigi* to a maximum heterozygosity of $H=0.048$ found in one of the populations of *Ctenomys talarum*. In general, the "Corrientes group" showed much lower heterozygosity values ($H=0.01$) than the "Mendocinus group" ($H=0.036$). This low variability within the northern group seems to run parallel to the low genetic divergence found among its pooled species. Average Nei's genetic distance within the "Corrientes group" is $DN=0.049$ which is a very low D-value for rodent species. On the contrary, a higher differentiation is found among the species conforming the "Mendocinus group" where $DN=0.146$, with minimum values of $DN=0.009$ between two populations of the species *Ctenomys talarum*, and $DN=0.270$ between two different species *Ctenomys talarum*, and *Ctenomys australis*. The highest average divergence, considering all the species examined, was that of *Ctenomys yolandae*, $DN=0.270$ (minimum $DN=0.207$ and maximum $DN=0.415$).

Nine restriction enzymes were used in the RFLP analysis of mitochondrial DNA, giving a total of 31 haplotypes. MtDNA divergences among the species included in the "Corrientes group" are lower than those among the remaining species, even when considering the "Mendocinus group", therefore supporting the allozyme results.

Our results point to a clear case of disjunction between the degree of chromosome variability and variation at genic level: the species of the northern "Corrientes group", which were defined on the basis of an extremely high diversity in chromosome number, show very little genetic variation or differentiation. This leads us to doubt the validity of the specific level of many species of the genus *Ctenomys*.

304 What to do when selection fluctuates : gamble, save, ... or both ? p11

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I. Phenotypic models of fluctuating selection :

Several classical models examine the problem of maintaining polymorphism under a fluctuating selection, through comparison of a constant gain (saving) strategy versus a stochastic gain (gambling) strategy. Haldane & Jayakar (1963) concluded that polymorphism was not possible in a haploid model (but it was in a diploid model). MacNamara (1980) used an ESS approach to a similar model (the *one-armed bandit*) : with additive gains, a pure strategy always wins. We developed a phenotypic model with mixed strategies, considering multiplicative gains. We showed that in this case, the ESS may be a mixed strategy, in intermediary selection conditions that we precise : the geometric mean fitness of the gambling strategy must be superior to unity, and the inverse of the harmonic mean must be lower than unity.

II. A possible application : cyclical vs. obligate parthenogenesis (in aphids, daphnia...) :

Such models can be applied to the case of cyclical parthenogenesis (*c.p.*). In aphids, for example, the sexually produced eggs are the species form of resistance to cold, and confer a rather constant winter fitness, while obligate parthenogens (*o.p.*) play a risky strategy (high reward in mild winters, high losses in cold winters). The variability in winter severity may then lead to a polyphenic equilibrium in intermediate selective conditions. In daphnia, a similar situation may be found in temporary ponds submitted to a risk of drought ; the sexually produced eggs which are the resistance form to drought represent a "play it safe" strategy vs. the gambling strategy of continuous clonal reproduction.

We propose a model based on experimental data on the genetic determinism of the type of life-cycle in an aphid species (Simon, 1991). *O.p.* generally keep the ability to produce males, a character that seems to be recessive while *c.p.* is dominant. We show that the polymorphism is still possible, though in a more restricted area of selective conditions than in the phenotypic model. This polymorphism is dynamic (the alleles frequencies being not fixed). Such system is extremely original since the exchanges between the sexual/asexual compartments are bi-directional ; *o.p.* may participate to the sexual reproduction (through their males), transmit their genes, and guarantee a minimum fitness in case of unfavourable conditions.

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T8

The "shape" of female mating preferences in a bushcricket.

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The "shape" of female mating preferences (or the "preference function") is an important component of models of sexual selection and communication. Whether preferences are directional or stabilising can influence the dynamics of the communication system. The extent of overlap between the shape of preferences and the current distribution of male traits will determine the strength of sexual selection on male traits and can indicate the extent to which coevolution, species recognition or arbitrary sensory biases may have influenced the evolution of the communication system. Here I describe experiments designed to assess the distribution of preferences and traits using the phonotaxis - calling song interaction of the bushcricket *Ephippiger* as a model system. Results indicate that the shape of preferences varies with different structural components of the signal. One major component is characterised by apparently broadly coevolved female preferences. Another is subject to directional preferences (resulting in preference for young males), while another has a pronounced mismatch between signal and preference with the most preferred signal component being well outside the range of the species. These results indicate that, while some traits are probably recognition signals which have evolved by coevolution, others are subject to "sensory drive". One female bias could be adaptive. In conclusion, female preferences can be complex and multivariate in nature. Even in an apparently simple communication system, different components of a signal can be subject to contrasting selection pressures from preferences.

CELLULAR MECHANISMS OF RESORPTIVE PROCESSES IN THE DEVELOPING SKELETON IN THE DIFFERENT CLASSES OF VERTEBRATE

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We described the comparative aspect of the resorptive processes in the chondral and bone tissue during skeleton morphogenesis in the amphibian, reptilian, bird and mammalian specimens. Despite the specificity of these processes in the vertebrate of the different classes it was established that the cellular mechanisms of resorption remain the same. By the electron microscopic and cytochemical studies, in the vascular canals of cartilaginous epiphyses and in the zones of endochondral process of bones, there were revealed monocytes, macrophages, the cells of the intermediate differentiation stages among the perivascularly located forms. In the lysosomes as well as on the surface of cytoplasmic membrane of mature macrophages the activity of acid phosphatase and non-specific esterase was demonstrable. Phagolysosomes showed accumulation of ^{35}S -sulphate label 2 hours after its injection into an organism. Macrophages cause degradation of non-mineralized cartilaginous matrix by secreting hydrolases and other enzymes and then phagocytize the preformed substrate. In the zones of endochondral process, macrophages also penetrate into the "capsules" of hypertrophic chondrocytes and are involved in their destruction. The cells are regarded as tissue-specific macrophages - chondroclasts. The mineralized matrix of the bone and cartilage is resorbed by multinuclear osteoclasts.

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T 11

The Evolution of Genetic Correlations: An Analysis of Patterns

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The genetic correlation is a central parameter of quantitative genetics, providing a measure of the rate at which traits respond to indirect selection (i.e. selection that acts not upon the traits under study but some other trait with which they have genes in common). In this talk I review the pattern of variation among four combinations of traits: life historical x life historical (LxL), morphological x morphological (MxM), life historical x morphological (LxM), and behavioral x behavioral (BxB). A total of 1798 correlations, distributed over 51 different animal and plant species, were analyzed. Because selection will tend to fix alleles that show positive correlations with fitness traits, correlations between life historical traits are predicted to be more often negative than those between morphological traits. This prediction is supported, the ranking (decreasing proportion of negative correlations) being $LxL > LxM > BxB > MxM$. The mean magnitude of the genetic correlation shows little variation among morphological and life historical combinations, and the distribution of values is remarkably flat. However, the estimated standard errors and the coefficient of variation (SE/r_G) are large, making it difficult to separate biological factors influencing the pattern of dispersion from experimental error. Analysis of the phenotypic and genetic correlations suggest that for the combinations MxM and LxM, but not LxL or BxB, the phenotypic correlation is an adequate estimate of the genetic correlation.

Selection on selfing rate in structured populations

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Previous theoretical studies of the evolution of the selfing rate have shown that mixed mating systems are not evolutionary stable states. Such models have however not included the effects of population structure and thus biparental inbreeding together with the evolution of selfing rates and inbreeding depression. In order to examine selection on selfing rates in structured populations, a stochastic model simulating a finite population with partial selfing and restricted pollen and seed dispersal has been developed. Selection on the mating system was followed by introducing modifiers affecting the selfing rate. The major result was that, with density dependent recruitment, a process which maintains the population structure necessary for biparental inbreeding to occur, a mixed mating system could be maintained. This result was associated with an increase of the mutation load with high selfing rates and, the selected selfing rate depended on the degree of population structure rather than on the initial selfing rate. With low dominance of deleterious alleles, complete allogamy can be selected for. Further studies showed that the more general condition of spatial heterogeneity of recruitment can lead to similar results, the most important condition being the maintenance of genetic structure within populations. A brief survey of the empirical literature shows that a positive relationship between the magnitude of inbreeding depression and the inbreeding coefficient within populations has been observed, in support of the present model.

Population structure of an alpine chrysomelid beetle - what scale matters?

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Herbivorous insects with their strong association to host plants often show very patchy distributions. On what scale "gaps" between suitable host plants/host plant patches are barriers to gene flow and affect population structuring depends on the dispersal of the species.

We addressed this question with two closely related leaf beetle species, *Oreina cacaliae* and *O. speciosissima* (Coleoptera, Chrysomelidae). Both can occur sympatrically on the same host plants at the same sites, but show different abundances in the field. Since direct observations of long distance dispersal of insects are almost impossible, we took first an indirect approach and tried to draw some conclusions from the genetic structure as revealed by allozyme electrophoresis.

The sampling was done in a hierarchical design, patches within localities (distances < 5km), localities within regions (distances 20 - < 400 km) and regions within the western species range (from the Pyrenees to Czechia). Analyses of 23 presumptive loci encoded by 17 enzyme system revealed that most differentiation already occurs between patches. Correlation of genetic distances (Nei's genetic distance) with geographical distances is significant. Indirect measures of gene flow suggest low gene flow between patches. In summary, both species show considerable genetic differentiation at a very small scale with evidence for restricted gene flow and isolation by distance.

DnaSP, DNA sequence polymorphism: an interactive computer program for estimating Population Genetics parameters from DNA sequence data

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DnaSP, DNA sequence polymorphism, is an interactive computer program package for the analysis of DNA polymorphism from nucleotide sequence data. The program, addressed to molecular population geneticists, calculates several measures of DNA sequence variation within and between populations (with and without the sliding window option), linkage disequilibrium parameters (including two different tests to determine whether the associations between polymorphic sites are or not significant), and Tajima's *D* statistic. DnaSP can automatically read two types of Input Data File formats: NBRF/PIR and MEGA formats. In both cases two or more homologous and aligned nucleotide sequences should be included in just one file (ASCII file). The output is displayed in three kinds of windows: text, grid (the output data are laid out in rows and columns like in a spreadsheet application), and graphic (scattergraph and line chart). The results can also be saved in a file (that can be used as input for other programs), or sent to the printer.

The program, that is written in Visual Basic v. 3.0 and runs on a IBM-compatible PC under Windows, can handle a large number of sequences of up thousands nucleotides each.

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T 17

Speciation through hybrid zones: Gene flow, Haldane's rule and imprinting

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To understand speciation it would seem useful to have as much information as possible on the spatial genetic structure of taxa that are considered good species. It is becoming increasingly apparent that species across their range are often divided into patchwork of parapatric subspecies and races, and where two forms meet, mate and hybridize, a hybrid zone occurs. Moreover, it is necessary to maintain the hybrid zone through time that the hybrids live close to the parental forms; they would show only partial sterility, and they could cross with the parental forms.

A range of questions should be asked of any hybrid zone in order to understand its status, and thereby proceed to the more general questions of genome differentiation, racial distribution and speciation. On view of this, studies have been focused on such a zone in the grasshopper Chorthippus parallelus in the Pyrenees. Two subspecies are present on the continent, C. parallelus erythropus found in the Iberian Peninsula and C. parallelus parallelus being widely distributed throughout in the rest of Europe. The hybrids between both subspecies of Cp fulfil all the characteristics mentioned above.

Some cytogenetic characters localized on the sex chromosome allow distinction between both subspecies and hybrid individuals. These characters have been studied in natural populations and backcrosses, especially the gene flow effect and the transmission of the sex chromosome to the next generations. The effect of heterochromatin conformation and sex linked genes will also be discussed.

How do longlived seabirds avoid over-investing in their offspring?

Bernt-Erik Sæther, Torkild Tveraa og Reidar Andersen.

According to life history theory, we would expect that longlived seabirds should minimize the effects of reproductive investment on future survival. This paper presents a summary of both empirical and experimental studies on the antarctic petrel *Thalassoica antarctica*. The aim has been to study the mechanisms that regulate reproductive investment. The antarctic petrel is a medium-sized seabird (5000 g) that only breeds on the Antarctic continent. It is suitable for studying investment in breeding because it has to fly at least 400 km over land to feed its offspring and lives in a rather hostile environment.

Our data show that body size is an important determinant of reproductive success: large birds are more successful than small birds. When the body condition of the parents is artificially changed, they invest more in their chances for future survival at the expense of a reduction in the provisioning rate of food to the chick.

The parents spend long period on the sea. During that period the egg or the small fledging are warmed by the other adult, which then continuously loses weight. Experimental evidence suggests that when the rate of energy requirements do not exceed a certain threshold, some individuals are willing to reduce their body condition to a very low threshold while waiting on the mate. Large individuals are willing to invest more than small ones.

Our results that an understanding of the factors influencing body condition may be important when examining the adaptive significance of variation in seabird life histories.

Fluctuating asymmetry in the chromosomal races of house mouse in Tunisia and their hybrids.

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Previous studies have demonstrated that two chromosomal races of the house mouse occur in Tunisia, one consisting in mice carrying the 40 acrocentric standard karyotype and the other represented by a Robertsonian (Rb) race ($2n=22$), homozygous for nine centric fusions. Allozymic divergence indicated that 22Rb mice presented a reduced level of genic variability resulting in genic differentiation from local standard populations with hybrids showing intermediate levels. The Rb populations are restricted to cities of central Tunisia whereas the 40 acrocentric mice occur in rural villages. Hybrids occur at the contact zones between the two habitats and exhibit an impairment of fertility leading to complete sterility in some individuals.

We report here a study on the developmental stability, estimated by the fluctuating asymmetry of dental measurements, of the two chromosomal races and their hybrids. The data show an increase in tooth size and a reduction in fluctuating asymmetry in hybrids. These results indicate that hybrids are developmentally litter than either of the parental races. Such changes in size and fluctuating asymmetry may result from a heterotic effect suggesting that the genetical divergence between the two races may be higher than that predicted by allozymes. Moreover, this study provides further evidence of the independance between developmental stability and fertility.

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T8

Female-female competition and the role of females in influencing mating patterns.

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The role of females in influencing mating systems has usually received less interest than that of males. Nevertheless, the behaviour of females may have substantial effects on the evolution of mating patterns. Already mated females may use various ways to reduce the mating success of their mates. Intrasexual competition among females and its effect on the mating system was studied in the European starling (*Sturnus vulgaris*). Females suffer fitness costs when mating polygynously because males contribute less in incubation and nestling feeding. Already settled females may minimise these costs by preventing the settlement of other females. Mated females showed strong aggressive responses against intruding females. The peak in aggression is associated with the settlement of secondary females, suggesting that female-female aggression is used to prevent or delay females from mating with the same male. Breeding interval between polygynously mated females was negatively related to the distance between their nests and experiments demonstrated that the distance between nest sites also affects the possibility for males to attract additional females.

PRELIMINARY DATA ON GENETIC DIFFERENTIATION BETWEEN
FRESHWATER CRAYFISH

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P7

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Natural populations of two species of freshwater crayfish, *Austropotamobius pallipes* and *Astacus leptodactylus*, previously included within the same genus (*Astacus*), were investigated by isoenzyme analysis of 15 loci.

Au. pallipes has an European range with three subspecies, whereas *As. leptodactylus* is found in Eastern Europe, Greece, Turkey and Siberia. The Italian taxon, *Au. pallipes italicus*, distributed from Calabria to Dalmatia, is severely endangered by pollution and habitat disturbance (IUCN Invertebrate Red Data Book 1983), which has drastically reduced its suitable habitats. Crayfish reintroduction was carried out in Italy by the immission of Turkish *As. leptodactylus* specimens.

The comparison of autoctonous *Au. pallipes italicus* and introduced *As. leptodactylus* showed that the two species are genetically differentiated at 9 out of the 15 loci studied, with a Nei average genetic distance of 0.91, a value often found between congeneric species. Similar levels of genetic variability were observed in the two species: a) expected mean heterozygosity (H_e) = 0,11 and 0,12 in *Au. pallipes* and *As. leptodactylus*, respectively; b) percent of polymorphic loci about 0,27 in both species. Some taxonomic and ecological aspects of genetic data are discussed.

GENETIC STRUCTURE OF THE HYBRIDOGNETIC *RANA ESCULENTA* FROM ITALY

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The genetic structure of 68 populations of the hybridogenetic water frog *Rana esculenta* from Italy and Sicily was investigated by isozyme analysis of 25 loci. *R. esculenta* specimens were identified on the basis on their genotypes at eight diagnostic loci, which show distinct alleles in the parental species *Rana lessonae* and *Rana ridibunda* and are heterozygous for both alleles in their hybrid derivative *R. esculenta*. The analysis of genetic variation in the hybridogenetic populations showed a widespread variability of the *ridibunda* genome (which is clonally transmitted through generations), at the loci *Ldh-1*, *6Pgdh*, *Aat-1*, *Aat-2*, *Pgm-2*, *Gpi-2*. Eighteen different hemiclones were identified, differing from each other at 1-3 loci, with a maximum of six different haplotypes per population. Eight hemiclones showed a *lessonae* allele at one or two of the diagnostic loci, while the remaining 10 showed "new" alleles, not found in Italian *lessonae* or *ridibunda* genomes, at 1 or 2 diagnostic loci. The observed hemiclinal variability could be caused by: i) local mutation; ii) multiple colonization by *R. esculenta*; iii) premeiotic recombination events, leading occasionally to the inclusion of a *lessonae* chromosome in the clonal *ridibunda* genome (Tunner & Heppich Tunner, 1991); iv) meiotic recombination in triploid *R. esculenta* (Hotz & Beerli, 1989); v) meiotic recombination of *R. ridibunda* specimens originated from occasional *R. esculenta* x *R. esculenta* matings (Hotz et al., 1992). The survey of about 4,000 specimens of the *R. esculenta* complex did not reveal the presence of *R. ridibunda* in Italy; however, a few specimens homozygous for *ridibunda* alleles at 1-3 loci were detected. The various hypothesis for hemiclinal variation in *R. esculenta* are discussed and its possible adaptive significance is examined, also in relation to the evolutionary success of this species in disturbed areas.

317 DISCRETE PACKING OF SPECIES AND TAXON CYCLES

T1

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We examine two models focused on the pattern of character distribution in the evolutionarily stable (ES) community/population. — *Species Packing*: In the first, we consider the interspecific competition along a resource axis, with each species specialized to a niche position with a fixed niche width. In spite that we allow continuum of species to invade, the ES community should consist of a finite number of species with distinctly separated characters. This makes a sharp contrast to the continuum of coexisting species predicted in the previously developed models. Prey-predator or host-parasite interaction could complicate the dynamics, but the ES community again consists of a discrete set of species in each trophic level. — *Body Size Evolution*: In the second, the body size evolution is modeled assuming that intraspecific competition favors larger size but the viability selection favors an intermediate. We assume a small extent of uncertainty and cost to the payoff for the contest between individuals of similar sizes. This is enough to preclude any continuous distribution from ESS. Instead, the ES population either be in stable polymorphism of distinctly different sizes, or cycles indefinitely between discrete set of sizes. The model therefore suggests that discrete size polymorphism is expected to evolve even if there is no physiological or developmental cost of producing continuous size variations, and that sudden shifts could occur in body size evolution as a result of intraspecific competition.

Characteristics of Cytoplasmic Cross Incompatibility in the Parasitoid Wasp
Nasonia (=Mormoniella) vitripennis.

[18] Saul GB

IT 14

Cytoplasmic incompatibility was first found in Nasonia in the mid-1950's when the frequency of hybrid (female) progeny from crosses of wild type males to females of stocks carrying the eye color genes peach (pe) and tinged (ti) dropped from the normal 85% to nearly 0%. The reciprocal crosses yielded normal frequencies of hybrid female progeny. Since then, other wild type and mutant stocks have acquired incompatibility similar to the types that appeared in the pe and ti stocks.

The incompatibility is maternally transmitted, persisting through fifteen generations of backcrossing. It is not accompanied by the presence of dead embryos, larvae, or pupae. No evidence of nuclear control has been found. The incompatibility has been found only in stocks inbred for many generations in the laboratory, not in stocks when first introduced into the laboratory.

When wild type sperm enter eggs of incompatible females, the first visible difference from normal fertilization is the appearance of a tangled mass of chromatin: the chromatin of the sperm.

The factors that cause the incompatibility can be inactivated by tetracycline, and can be transferred to wild type stocks or to "aposymbiotic" stocks created by tetracycline treatment. Transfer can be by injection of crushed eggs of incompatible stocks into wild type or aposymbiotic females, or into the hosts on which they feed. Contact with the crushed eggs may also cause transfer to aposymbiotic females.

The incompatibility factor can be cultured in chick egg yolk sacs, and may be a bacterium of the Wolbachia group. An additional, smaller, agent may also be involved.

319.
Genetic basis of flowering time variation

IT4

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Adaptation of plant populations to their local environment is often due to quantitatively varying traits. While they can be analysed in the framework of quantitative genetics, it has until recently been difficult to find the loci responsible for the variation. We want to find out the genetic basis of the variation. In addition to examining candidate loci, we can use QTL mapping to locate the loci. In most cases, QTL mapping has been done in crop plants (and animals). We have examined flowering time in a natural population of the selfing annual Arabidopsis thaliana. If not vernalized, northern populations flower very late, whereas southern populations flower rapidly. The flowering times of Finnish and Central European populations differ by more than 100 days. The backcross of an F1 between the Finnish Naantali natural population and the German Limburg strain was analysed with respect to flowering time and molecular markers including RFLPs, RAPDs, CAPS (cleaved amplified polymorphic sites) and microsatellites. This analysis revealed two loci, at the top of chromosomes 4 and 5, with major effects of at most 20 and 7 days. Flowering time differences are influenced by vernalization, but even after full vernalization, differences remained.

319a.

TIG

Spatial structure as revealed by microsatellites in plants

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Microsatellite loci are highly polymorphic, they are found in all areas of the genome, and, being PCR-based, they can be analysed from small amounts of tissue. We have studied microsatellite variation in the selfing Arabidopsis thaliana and its outcrossing relative Cardaminopsis petraea. About one third of published microsatellite sequences of A. thaliana (Bell and Ecker 1994) function in the related species (as such, without any further optimizing of PCR conditions). The estimates of population differentiation obtained by allozymes, sequence variation, and microsatellites will be compared. Microsatellites developed for Pinus radiata (Smith and Devey 1995) function in P. sylvestris. Initial studies have shown that in a sample of 50 trees, 6 and 11 alleles could be found at the two loci studied, with the highest within population expected heterozygosity 0.85. The distribution of genetic variability between populations was as for other random molecular markers in Scots pine ($F_{ST} = 0.02$). The high genetic diversity offers much promise for within population studies.

Concordant vs. conflicting character sets in systematics: hints from *Dolichopoda*

IT 7

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The occurrence of differences in weight, significance, and even direction, between characters in assessing systematic relationships and tracing phylogenies at any systematic rank, is an issue long recognised by many systematists. Yet the significance and the management of concordant and conflicting data sets in systematics represents a continuing source for discussion and controversy. Types of character sets to be faced include molecules vs. morphology, qualitative vs. quantitative, adaptive vs. neutral, etc. A major issue of debate also concerns the problem of character selection and/or weighting.

A selected array of species in the cave cricket genus *Dolichopoda* has now been sufficiently investigated by different character sets to provide a robust source of empirical data for comparative analysis.

A formal test of congruence and conflict has therefore been performed on distance matrices derived from three multivariate sets of morphometric characters and four sets of molecular data including allozyme polymorphisms, mtDNA RFLP's, DNA-DNA hybridization data and sequences of highly repetitive satellite DNA. Congruences and conflicts between these data sets in tracing systematic relationships are highlighted and discussed in respect of their evolutionary meaning and scaling and their role as tools in phylogenetic analysis.

Highly repetitive satellite DNA as a molecular marker for phylogenetic analysis of the genus *Dolichopoda*

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Dolichopoda (Orthoptera, Rhaphidophoridae) cave crickets are distributed throughout the North Mediterranean region with populations usually isolated from each other, with very low, if any, levels of gene flow.

The evolutionary relationships within a sample of populations and species of cave crickets belonging to this genus have been so far investigated by means of several morphometric character sets and molecular markers with different informational value in respect of phylogeny and adaptation (Sbordoni et al., 1991). In order to get additional information we also started extensive studies on highly repetitive DNA, a class of DNA supposed to be fast evolving and selectively neutral (Bachmann et al., 1944 and in prep.). Tandemly repeated satellite DNA is typically non-coding and located in the heterochromatic regions of chromosomes. High intraspecific sequence homogeneity contrasts frequently high interspecific diversity. This is usually explained by the concept of "concerted evolution" (Dover, 1982). We have isolated and characterized a restriction satellite DNA, approximately 500bp in length, which can be detected in all *Dolichopoda* populations and species so far examined and that seems to be widespread throughout the entire genus.

Repetition units from 12 populations were isolated and cloned into plasmid vectors and about 50 clones were selected for further sequence analysis. A neighbor-joining phenogram generated from pairwise Kimura distances shows homogeneous clusters of sequences, that are consistent with the specific rank of populations and in agreement with those derived from other molecular markers such as allozyme polymorphisms, DNA-DNA hybridization data and mitochondrial DNA RFLPs. Species can clearly be discriminated, indicating a role for satellite DNA as a marker for cladogenetic events. However, sequences derived from different conspecific populations cannot be discriminated.

This suggests that specific evolutionary changes of satellite DNA in the genus *Dolichopoda* result from long term genetic isolation.

ASYMMETRIC STRAND MUTATION INDUCED BY METHYLASES

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Methylating enzymes are generally present at the level of the most primitive prokaryotes, and they seem to play a role in gene regulation also in those organisms as they do in eukaryotes (1). For instance, CpG methylation has been recently suggested to play a role in the evolution and stability of chromosome structure (2). However, methylation is also considered a common cause of mutation and base substitution. In particular, the frequent C.G→T.A transition is attributed to specific cytosine methylation, and it is possible to test, in rigorously orthologous proteins, whether there is an excess of CG→TG and CG→CA transitions as compared with other base substitutions.

In this study, the distribution of the twelve possible substitutions was studied in pairs of rigorously orthologous ubiquitins from eukaryote organisms. The C→T transitions, followed by a G, and G→A transitions, preceded by C were attributed to methylation on the sense and antisense strand respectively. It was observed that a significant excess (905) of C→T transitions, followed by a G in 3', exists in all organisms as compared to the (92) G→A transitions preceded by a C in 5'. Since the transition CG→TG indicates methylation of the sense strand, and the CG→CA methylation on the antisense, the ratio of sense: antisense transitions is 10:1. There seems to be strong indication that there is strand asymmetry in mutations presumably induced by methylation. The excess might be due to several processes, such as bias of DNA repair processes, bias of mutations at 5'-CG-3' sites in silent vs. non-silent mutations, or preferential methylation of the sense strand in eukaryotes.

In the analysis between species, three different matrices of nucleotide substitutions, corrected for multiple events at the same site, were obtained and used for constructing phylogenetic trees (by using the Average Distance Method): 1) a matrix for C/T transitions at CG sites, or "methylation" substitutions; 2) a matrix for all other substitutions or "residual" substitutions; 3) general matrix for the total number of nucleotide substitutions.

The comparison of the two phylogenies obtained from methylation substitutions and from residual substitutions shows that methylation mutations do not accumulate proportionally with time of separation as other mutations do. The phylogeny from methylation substitutions is not consistent with the evolutionary relationships of the organisms used, as the one from all other mutations. The distorting effect of the methylation substitutions is visible also on the phylogeny obtained from all mutations. Thus, we believe that by removing from the total substitutions those attributable to methylation, it is possible to improve the accuracy of phylogenetic trees obtained from sequence data.

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evolutionary change, smooth or jumping?

322a.

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Charles Darwin considered artificial selection as a model for evolutionary change. I intend to look at what modern experiments on artificial selection, predominantly with *Drosophila*, have learned us about genetic variability that is used for phenotypic change by selection. Is it smooth or jumping? Does it reveal discontinuities?

In the course of time complexities were observed which did not fit into the current theory. Instead of declining, genetic variability often increased during selection. Lethals and genes with large effect cropped up. Sometimes selection only succeeded into one direction. Localization of the genes accumulated by selection showed distribution over the whole genome but often a few loci contributed most of the selection response. The effect of the genes was in some cases strongly dependent on characteristics of developmental processes which could inhibit phenotypic change or lead to thresholdlike change.

Increasing population size extended selection progress but did not reveal new aspects of genetic variation, with the exception of the application of insecticides in natural populations. Do we miss important aspects of genetic variation in our small laboratory populations?

Recently it has been suggested that a large part of evolutionary change, and in particular genetic adaptation, is generated by single genes with large effect. But one has to be cautious when this is concluded from the endstage of a long process of selection.

Could differences which have to be bridged now by mutations with large effect nevertheless be explained by gradual selective change? What kind of artificial selection experiments could contribute to the solution of this kind of problems? Is it necessary to involve developmental genetic methods in the analysis?

Self-incompatibility and a positive correlation between heterozygosity and fitness in *Arabis petraea*.

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Positive correlations between individual heterozygosity at allozyme loci and fitness have been reported for many plant species. The two common genetic hypotheses for the phenomenon are (1) strict overdominance in fitness at loci, and (2) dominance in fitness at loci with linkage disequilibrium. We report results for *Arabis petraea* (Brassicaceae), a self-incompatible perennial with a circumboreal distribution. Heterozygosity at 9 polymorphic allozymes was correlated to morphological measurements of green house grown individuals, collected as seed families from two natural Icelandic populations. A highly significant positive correlation between heterozygosity and the growth measurements believed to correlate with fitness was found in both populations, and this could not be attributed to either the effect of maternal heterozygosity or the effect of progeny heterozygosity alone.

Empirical results are presented that indicate very restricted gene flow in *A. petraea*. The nature of the interaction between a sporophytic self-incompatibility system and population structure was therefore investigated with computer simulations. The results point to the sporophytic self-incompatibility system as important in shaping the above correlation, and this will be discussed in relation to the overdominance and the dominance hypotheses of heterozygote advantage.

Host shifts in parthenogenesis-causing bacteria

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Wolbachia bacteria are known or suspected to induce parthenogenesis in a wide variety of parasitic wasps. They cause unfertilised females to produce all-female offspring by disrupting the first mitotic division. This results in gamete duplication and, hence, diploidisation. The embryos produced follow the hymenopteran sex determination and develop into females.

This paper will discuss the degree of phylogenetic fidelity of these parthenogenesis-causing *Wolbachias*. Comparative molecular phylogenetics are performed both on the bacteria and their insect hosts, both intra- and interspecifically. These analyses provide insight into the frequency of host shifts.

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We are studying the evolutionary divergence of randomly isolated genes from *Drosophila melanogaster*. About one hundred different cDNA clones were isolated from an embryonic cDNA library. With these cDNAs we performed Southern hybridization experiments against genomic DNA from *D. melanogaster*, *D. virilis*, *Musca domestica* and *Tenebrio molitor* for a quick assessment of their degree of evolutionary conservation. To infer possible functions of the these cDNAs, the clones were partially sequenced and in situ hybridized against whole mount embryos of *D. melanogaster*. Furthermore, their level of expression in embryos was estimated.

The majority of these expressed sequences seems to be little conserved on sequence level and to evolve rapidly. About one third of the partial DNA sequences showed statistically significant matches in searches of sequence databases. They comprise a similar composition of different classes of genes which were found in other cDNA sequencing projects. Sequences with a match in databases tend to be more conserved than clones with unknown identity. Analysis of expression patterns showed that about a quarter of the unknown clones are transcribed in a spatially regulated manner. However, no relationship with their degree of evolutionary conservation could be detected.

Currently, we are investigating the molecular evolution of a subset of these cDNAs in more detail. This subset includes cDNAs which on Southern Blots appear to evolve rapidly, whose partial sequences do not give a match in databases and which exhibit a spatially restricted expression pattern or a low level of expression in the embryo. Their homologous transcripts were isolated from an embryonic cDNA library of the closely related species *D. yakuba* and the cDNAs from both species are being completely sequenced. Results of this work will be presented.

Nucleolus organizer regions and karyotypic evolution in the genus Ophryotrocha (Polychaeta)

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Species of the genus Ophryotrocha (Polychaeta, Dorvilleidae) have been widely used as a model for comparative studies on sex allocation patterns, reproductive strategies, mechanisms of speciation. Four out of the nine most studied species (i.e. O. notoglandulata, O. macrovifera, O. labronica labronica, O. labronica pacifica) have three pairs of chromosomes, two (i.e. O. diadema, O. puerilis) four pairs and three (i.e. O. robusta, O. gracilis, O. hartmanni) five pairs. From a karyological point of view the 9 species proved to be rather homogeneous. Their karyotype showed metacentric chromosomes only, apart from O. robusta where also a pair of acrocentric chromosomes was found (Robotti *et al.*, 1991). The haploid nuclear DNA content was 0.4 pg on average in 7 out of 9 species (Sella *et al.*, 1993).

To test whether such karyological homogeneity also involved the activity of the nucleolus organizer regions, silver positive patterns were analyzed in metaphasic plates of the nine quoted species.

Silverpositive regions were always terminally located in all but one species, O. diadema, where NORs were interstitially located. This pattern might have been originated in an ancestral species with $2n = 10$ chromosomes by means of a centric fusion of two monoarmed chromosomes, one displaying a terminal NOR and the other one without it.

According to the current interpretation of the evolutionary meaning of variation in silver stained regions, a single pair of NOR represents a plesiomorphic character, while more than one pair of NOR represents an apomorphic character. According to this hypothesis, karyotype of O. robusta should be considered as the most conservative within the genus because it shows a single pair of NOR chromosomes (as well as the hypothetical ancestral number of chromosomes). The ancestral condition seem to have been retained also in O. diadema and O. puerilis. In contrast, in O. gracilis and O. hartmanni the occurrence of a polymorphic silver positive pattern could indicate that the ancestral nucleolus organizers have been involved in karyotypic changes. The four species with six chromosomes have two chromosome pairs involved in nucleolus organization and display NOR polymorphisms. Therefore they can be considered as the most specialized within the genus Ophryotrocha.

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The small marine worm Dinophilus gyrociiliatus shows a very interesting case of female biased sex-ratio and a very remarkable mating system. This species has a sex chromosome system with male heterogamety of the X0-XX type. There is egg size dimorphism with males developing from small and female from large eggs and probably there is selective fertilization of large oocytes by X-bearing sperm and of small oocytes by sperm without sex chromosome. Sex determination is therefore progametic (Martin & Traut 1987). Eggs are laid in an egg capsule where female eggs are always in the majority (i.e. 3 : 1 on average). Males are dwarfed, without a digestive system and seldom leave the egg capsule. They inoculate their sperm into their immature sisters before the latter leave the egg capsule (Traut, 1969, 1970).

Charnov (1987) suggested that such a female biased sex ratio is just that which should be favored by natural selection when there is no random mating, according to the model of the Local Mate Competition (Hamilton, 1967). Therefore, if in a high density population strict sib-mating is relaxed a less female biased sex-ratio is expected.

We tested this hypothesis by examining the sex-ratio (i.e. the ratio of large to small eggs) of capsules laid by females reared at three population densities (0.1 ♀/ml, 1 ♀/ml, 2 ♀♀/ml) during the first three weeks of their fertile life (four week old females lay only capsules with a 1:1 sex-ratio). Experiments were repeated twice. For each experiment the number of observed capsules was about 1000.

At the population density of 2 ♀♀/ml the egg capsule mean sex ratio changed from 3:1 to 2:1. Correlation between the mean sex ratios and the population densities was significant at the 5% P level ($r = -0.89$; $0.05 < P < 0.01$). The fact that at 2 ♀♀/ml density sex ratio of the egg capsules becomes less female biased could mean that at such population density capsules are close enough for males to venture to other capsules and successfully mate.

Even if they show some moderate ability to modify egg capsule sex ratio, females of Dinophilus gyrociiliatus are unable to modify male and female egg size according to the capsule sex ratio. No statistically significant difference was observed between mean egg diameters of male and female eggs laid at 0.1 ♀/ml and 2 ♀♀/ml densities.

Spatial structures of grasshopper populations

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The analysis of species population distributions over regions, geographical landscapes and their units allows us to distinguish their groups with similar relations to ecogeographical characters, including environmental heterogeneity. It is essentially important for re-estimation of different ecologo-geographical barriers being the limits for species spreading. Completely isolated populations are exceptional. They may be observed for non-flying montane or island forms. Continuous populations with uniform structure are very rare too. On plains, we can describe at least three species population groups. These groups form the limited number of combinations in every concrete region or locality. We described 4 types of such combinations (Stebaev, Sergeev, 1982; Sergeev, 1986; Kazakova, Sergeev, 1992). Observed pattern may be essentially changed at various scales of studies. The analysis at the regional and basin levels usually shows that every part of range is a mosaic, where parcels of transitional, marginal and sometimes main types of settlement distribution intersperse throughout the dominating background.

Our data allow us to support an idea that really the majority of grasshoppers (including good flyers) and locusts do not crossed many inter- and intralandscape boundaries. As a rule, these boundaries are associated with difference of phenotypic traits of these insects. Such pattern is supposed to be general for temperate Eurasia, especially for arid and subarid regions. In this way, general population structures at various levels of studies should be evaluated and possible trends of microevolution may be estimated. The another thing is associated with understanding the problems of a biological diversity because we can evaluate both a taxonomic diversity and diversities of population and community types too.

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Trade-offs between life history traits and sexual ornamentsBen Sheldon, Lars Gustafsson and Anna Qvarnström*Section of Animal Ecology, Department of Zoology, Uppsala University,
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Both life history traits (e.g. clutch size, timing of breeding, parental investment) and sexual ornaments can be regarded as forms of reproductive investment that, all else being equal, are condition dependent. Consequently, one can expect trade-offs between life history traits and sexual ornaments. We investigated the existence of such trade-offs by performing brood manipulation experiments on pairs of collared flycatchers Ficedula albicollis and studying the effect that these manipulations had on the subsequent size of a sexual ornament (the white forehead patch) in males. The white forehead patch is positively related to several measures of condition in males and seems to be involved in signalling during aggressive encounters between males. We found a strong relationship between the degree of experimental manipulation of parental effort and the subsequent size of the ornament in males: males that had experimentally increased parental effort developed smaller ornaments in the following year and vice versa. In addition to this intragenerational trade-off, we found an intergenerational one: ornament size of male recruits was related to the experimental manipulation they had experienced during rearing. Thus males face a trade-off between their ornament size in future years and that of their sons. The fitness cost of smaller ornaments is not clear, but for unmanipulated males, between year changes in ornament size are positively related to changes in the number of females that they are mated to. Viewing sexual ornaments as subject to similar processes as 'classical' life-history traits provides insights into a number of areas, including age-related patterns of ornament variation and the relationship between certainty of paternity and paternal effort and also suggests a sensitive method for measuring the fitness costs of reproductive decisions in iteroparous organisms.

332 **Evolutionary consequences of sexually transmitted diseases for host reproductive strategies**

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Ben Sheldon

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Sexually transmitted parasites are widespread: well-studied examples are known from several vertebrate classes, arthropods and plants. As epidemiological models show that the number of, and variance in the number of, sexual partners are critical variables in predicting the spread of a sexually transmitted parasite, pathogenic sexually transmitted parasites may exert strong selection on host sexual behaviour. I discuss some possible cases and consequences of such selection. Further, selection to avoid infection by sexually transmitted parasites might explain why female vertebrates provide such a hostile environment for male ejaculates, and hence contribute to the commonly observed relationship between male sperm production and the frequency of multiple mating. This may also have interesting consequences for a special subset of good genes models of female choice. Because the risk of infection increases with the number of partners, hosts potentially exposed to sexually transmitted parasites face a special case of a current versus future reproduction trade-off. I discuss possible consequences of this for host reproductive strategies.

The evolution of ineffective antipredator behavior in a sunfish-salamander system. 334 T
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Field surveys and experiments demonstrated that streamside salamander larvae, *Ambystoma barbouri*, suffer heavy predation by the green sunfish, *Lepomis cyanellus*. Behavioral observations and a model that quantitatively linked antipredator behavior to predation rates suggested that the key prey 'ineffective' behavior is relatively high larval activity in fish pools in the daytime; i.e., if larvae hide they can survive well, but because they are over-active in fish pools in the daytime, they suffer heavy mortality. **The evolutionary mystery is thus: why have larvae not evolved to decrease the level of this key ineffective trait?**

Perhaps *A. barbouri* larvae respond poorly to fish because they lack a long evolutionary history with predatory fish. To test this historical perspective, we compared the antipredator behavior of *A. barbouri* to that of a sister species, *A. texanum*, that inhabits fishless, ephemeral ponds. Various lines of evidence suggest that *A. barbouri* is recently derived from an ancestor that probably resembled *A. texanum*. A phylogenetic constraint hypothesis predicts that due to selection from fish predation, *barbouri* should be less active than *texanum*, but that *barbouri* might still be too active because of its history of evolution without fish. Comparisons of the activity of the two species showed, however, that in all tested conditions (with or without predatory fish present), *barbouri* were more active than *texanum*. **That is, evolution has gone in the wrong direction as far as this key ineffective trait is concerned.**

Lack of evolution due to lack of genetic variation also appeared unlikely to be an important constraint on the evolution of inappropriately high activity in the presence of fish because larvae did evolve (based on the comparison between sister species) and because full sib analyses revealed significant variation in key antipredator traits in both species.

Instead, **the key constraint shaping the evolution of activity levels in these larvae appeared to be behavioral correlations across situations.** That is, the same individuals (and sibships) that tended to be active in the absence of fish were also inappropriately active in the presence of fish, and the same individuals (and sibships) that were best at hiding (least active) in the presence of fish were also relatively inactive in the absence of fish. We refer to these as 'fast' and 'slow' larvae. In streams that consist of a mixture of fish and fishless pools, strong selection favoring high activity (fast larvae) in fishless pools (high activity translates to high feeding, growth and developmental rates) apparently overrides selection favoring low activity in fish pools. The overall result has been the evolution of fast larvae with a concomitant inability to cope well with predatory sunfish.

An additional factor influencing the evolution of behavior in this system is gene flow among populations. Isolated populations showed local adaptation; an isolated population that co-occurs with fish showed lower activity and stronger responses to fish than an isolated population in a fishless stream. In contrast, two populations that experience different selection pressures (one with fish, the other without fish), but also considerable gene flow, did not significantly differ in antipredator behavior. That is, gene flow can further limit local adaptation to predators and thus also help to explain the existence of ineffective antipredator behavior.

SIMMS, ELLEN L. University of Chicago, Dept. of Ecology and Evolution, 1101 E. 57th Street, Chicago, Illinois, USA, 60637. Costs and benefits of plant responses to herbivores and pathogens.

Plants exhibit various evolutionary responses to tissue damage caused by disease or herbivory. Traits may arise which reduce the level of damage, either through resistance or avoidance, or plants may evolve mechanisms for tolerating damage by reducing its effect on fitness. Resistance is defined as the ability of a plant genotype to reduce tissue damage by grazers or parasites (including disease) relative to other genotypes. Tolerance is defined as the ability of a plant genotype to sustain a particular level of tissue damage with relatively less fitness decrement than other genotypes experiencing the same level of damage.

Coevolutionary cost-benefit models predict that an important constraint on the level of quantitative plant resistance to phytophages is the pleiotropic fitness cost associated with allocation of resources to defense. Similarly, intermediate levels of tolerance may be maintained by pleiotropic fitness costs of allocation to compensatory growth and reproduction.

A field experiment was performed to detect fitness costs in the common morning glory, *Ipomoea purpurea*, of resistance to and tolerance of anthracnose, a leaf-spotting disease caused by the pathogenic fungus, *Colletotrichum dematium*. This experiment yielded no evidence that resistance to anthracnose involved direct fitness costs. Nevertheless, the fitness of diseased plants was negatively genetically correlated with the fitness of uninfected control plants. This result could be explained largely by the detection of fitness costs associated with disease tolerance. I will discuss several implications of these results for the evolution of plant responses to herbivores and pathogens.

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Due to a number of factors, the native Caledonian pinewood of Scotland now covers only 5% of their former range. They exist as a series of small widely scattered remnants in which *Pinus sylvestris* L. is the dominant component and constitute one of the only remaining natural ecosystems in Britain. Despite their limited distribution, the remaining pinewood sustain high levels of biodiversity and for this reason as well as their undoubted aesthetic cultural and historic qualities, they have become a significant priority for a number of conservation agencies.

One of the most urgent priorities in terms of conservation, is to strike a balance between maintaining the variation found in the Scots pine populations and the "native" aspect of the remnants. Monoterpenes and isozymes data have been used to develop guidelines and conservation programmes for management of the remaining pinewoods, but this information has inherently limited value as most variation resides within populations rather than between them.

The development of techniques used in molecular biology will significantly increase the levels of both detection and quantification of variation, and will allow the study of selective neutral genetic variation. The distribution of this material is however, strongly influenced by interpopulation gene flow via pollen and seed. In *P. sylvestris* pollen flow between populations is substantial and therefore biparentally inherited nuclear markers or paternally inherited chloroplast markers would show a low degree of interpopulation differentiation. The mitochondrial genome of *Pinus* however, is maternally inherited and as such would be expected to show a higher degree of interpopulation variability as seed movement between the remnants is relatively infrequent. This population-specific variation can readily be detected using techniques developed in molecular biology, such as Restriction Fragment Length Polymorphism (RFLP) analysis and Polymerase Chain Reaction (PCR)-based methods.

Total DNA is extracted from *P. sylvestris* buds or needles, digested with a series of restriction endonucleases, electrophoresed and Southern blotted onto nylon membranes. Hybridisation with homologous probes then follows and RFLP patterns examined. These can then be used to build up a "genetic register" of all the remnant populations.

PCR and mtDNA specific primers can be used to amplify fragments of mtDNA from individuals of the different native pine populations which are then screened either directly or after restriction digestion. These are also screened for variation between the remnant populations.

This work is being carried out on a number of native Scots pine populations and results so far will be presented.

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Hamilton and Zuk suggested in 1982 that sexual ornaments evolved through sexual selection as indicators of parasite resistance. As a mechanistic explanation to why sex traits should reflect parasite resistance, the "immunocompetence handicap" hypothesis suggests that development of sexual ornaments have costs to immunity. Sexual hormones, such as testosterone, have a dual effect; they induce development of sexually selected traits, while simultaneously suppressing the immune system. Here we present a novel idea to account for this seemingly maladaptive effect of sex hormones. Spermatozoa are considered "non-self" by the immune system. Therefore, auto-immune attacks from the immune system on gonads occurs and may influence fertility. Thus, given the adverse immunological effects on sperm, individuals must suppress immune function during spermatogenesis. This is an adaptive explanation for the immunosuppressive effects of sex hormones. The consequences this may have had in the evolution of signals in sexual selection is discussed.

Salt adaptation in a constant or (temporally or spatially) varying environment.

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Plantago coronopus, the Buckshorn Plantain, is mainly growing in the coastal zone, where it is exposed to fluctuating concentrations of NaCl. These habitats are characterised by a highly variable abiotic environment, both in space and time. As a reaction to salt, organic solutes (sorbitol in particular) accumulate, probably to cope with osmotic stress.

In an artificial selection experiment, plants are grown under four different selective environments, two constant (salt or non-salt) and two varying. Variation in space was imposed by alternating selective environments (salt or non-salt) between generations and variation in time by alternating environmental conditions within one generation. Plants were selected after four weeks, based on their number of leaves, a characteristic expected to be related to plant performance.

Questions are:

- Is there genetic variation for the selected component?
- Do different lines change in salt adaptation?
- Are there changes in plasticity of salt adaptation in the different selective environments?
- Are there changes in sorbitol synthesis, as a correlated response?

The experiment still runs, but after three generations it seems that genetic variation for the selected component is available.

- It is predicted that the lines selected in the varying environments will become more plastic than the lines selected in the constant environments.
- For sorbitol synthesis, it is expected that lines selected in a constant environment may change their constitutive levels, whereas in variable environments selection results in inducible concentrations and higher plasticity.

Paternity and paternal care in polygynous European starlings, *Sturnus vulgaris*.

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Among animals, parental care by females is more widespread than parental care by males. A lower certainty of relatedness to putative offspring for males than for females have been suggested to be important in the evolution of parental care. How much a male invest in parental care is thus expected to increase in relation to the certainty of paternity. When faced with a reduced paternity in a brood, a male bird may act in one of several ways. He may commit infanticide to entice his mate to produce a new clutch in which his paternity is higher. Alternatively he may ignore the brood or adopt it but reduce his parental investment. In this study the choices made by polygynous male European starlings *Sturnus vulgaris* when facing reduced paternity were studied. The expected paternity for polygynous males in one of their broods were experimentally manipulated and the resulting paternity evaluated using DNA fingerprinting. When paternity was predictably low and the likelihood that females rapidly produced replacement clutches was high males committed infanticide. When paternity was predictably low but also the likelihood of a replacement clutch was low, males ignored the broods. When the threat against paternity was intermediate, males adjusted their level of parental investment to the expected paternity in the brood. This study, thus, demonstrates that male starlings have an array of behaviours to cope with variation in paternity.

Evolutionary radiations in echinoderms: a comparison of larval and adult diversification.

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Echinoderms pass through two very distinct and contrasting phases during their life history, a benthic adult stage and a planktonic larval stage. Furthermore, the metamorphosis that occurs between larval and adult stages entails complete anatomical reorganization. We know much about how adult morphology has evolved because of the fossil record, and this reveals that changes have occurred erratically over time. In contrast, there is no fossil record of larval forms for comparison and so we cannot tell directly whether larval evolution occurred largely independent of, or in tandem with, evolution of adult morphology.

It is, however, possible to compare and contrast patterns of larval and adult morphological evolution from the analysis of character distribution amongst extant forms, given a reliable phylogeny for the group. Phylogenetic hypotheses are now available for a number of echinoderm groups based on ribosomal RNA sequence data and in many cases these are congruent with morphology-based phylogenies, giving greater confidence that the postulated relationships are correct.

Using well-supported phylogenies I investigate how larval and adult evolution compare and contrast during two radiations; the post-Palaeozoic diversification of echinoids and the early Palaeozoic diversification of the five echinoderm classes. These analyses reveal that larval and adult stages of life history have been evolving largely independently and that the establishment of adult body plans and larval body plans are unrelated.

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FREQUENCY-DEPENDENT FITNESS AND THE EVOLUTION OF FLORAL TRAITS THROUGH POLLINATOR BEHAVIOUR PATTERNS

Floral corolla traits in insect-pollinated plants are frequently polymorphic for characters such as colour, scent and size. Frequency-dependent selection (FDS) has been suggested to be one of the most important mechanisms by which polymorphisms are retained in populations, and the potential for pollinating insects to exert FDS on corolla traits, particularly on corolla colour, have been investigated. An experimental approach was adopted, using captive colonies of bumblebees *Bombus terrestris* foraging on arrays of artificial flowers of two or three morphs which are varied in frequency and in nectar availability. It will be shown how and when pollinators do forage in a frequency-dependent way, and how this behaviour is influenced by factors such as nectar offered by different floral morphs and by pollinator experience. In addition, the order in which flowers are visited by pollinators is non-random, and the potential for pollinators to induce assortative mating will be discussed. We consider the consequences of such pollinator behaviour for evolution of floral corolla traits: pollinators can induce either positive FDS on floral traits by preferring common corolla colours, leading to monomorphism, and also negative FDS by preferring rare corolla colours, thus leading to polymorphism.

Cuckoo host selection; characteristics determining the selection of the host
the European cuckoo (Cuculus canorus)

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It is known that not every species is used as host by the European cuckoo (Cuculus canorus). Some potential host characteristics are commonly regarded suitable for rearing young cuckoos. Some host characteristics are insectivorous, open-nesting, laying of small eggs, building of shallow nest cups. However, works are available which have analysed host characteristics in relation to parasitism rate by the European cuckoo.

We have used 73 species of European passerines as potential hosts. These, information was available in the literature on all the following variables: 1) parasitism rate (dependent variable), 2) host density, 3) body mass, 4) clutch size, 5) incubation period, 6) duration of host parental care for their own chicks (nesting plus fledging period), 7) brood reduction strategy (yes or no), 8) type of nest (open, semi-open or hole-nesters), 9) sociability (solitary, semi-colonial or colonial) and 10) food type that host brings to nestlings. To create a continuous canonical axis with the discrete variables (7, 8, 9 and 10), we carried out a canonical correspondence analysis and later used the coordinate value of each species to compute the comparative analysis of the host characteristics (discrete and continuous variables together) using Felsenstein's (1985) independent comparison method to control for the common phylogenetic descent.

The results of the analyses showed that the density of the host species was the variable with the strongest relationship with parasitism rate (partial correlation coefficient $r = 0.379$, $p < 0.0015$) followed by the duration of parental investment period (partial correlation coefficient $r = -0.278$, $p < 0.02$) and the kind of nest, selecting the open nesters (Canonical axis 1, $r = 0.232$, $p = 0.05$). These three variables accounted for 25% of the variance (multiple $r^2 = 0.7545$, $d.f. = 3, 68$, $p < 0.0002$). However, the duration of the parental care period could be related to the kind of nest used, given that hole-nesting species normally have a longer nestling period than the non-hole-nesters (perhaps because of the reduction in predation risk). Therefore, we reanalysed the data ignoring the hole-nesters, but the results were the same. The variable best related with the parasitism rate was the host density (partial correlation coefficient $r = 0.368$, $p = 0.005$), followed by the duration of parental care (partial correlation coefficient $r = -0.296$, $p < 0.02$), both variables together representing 21% of the variance (multiple $r^2 = 0.455$; $F = 7.042$, $d.f. = 2, 54$, $p = 0.00192$).

Therefore, the cuckoo selects its hosts on the basis of their availability and it prefers those which have a short breeding period. Perhaps the reason the insectivorous variable did not prove significant in the analysis was because most of the passerine species used feed their chicks insects, and the variance was too small to be related to the different parasitism rates.

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PHENOTYPIC PLASTICITY OF GROWTH AND SURVIVAL IN THE COMMON LIZARD (*LACERTA VIVIPARA*)

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Phenotypic plasticity is a pervasive phenomenon in animals and plants indicating the faculty of a given genotype to express different phenotypes across different environments. In some cases, phenotypic plasticity can be interpreted as a response to cues heterogeneously distributed across environments, response which may result in selective advantages for the individuals expressing it (e.g., predator-induced changes in both invertebrate and vertebrate prey morphology). In some other cases, phenotypic plasticity may however simply reflect non adaptive responses to proximal environmental factors (e.g., temperature effects on ectotherm developmental time).

We investigated sources of variation of growth and survival in two populations of *Lacerta vivipara* from Northern (Brittany) and Southern France (Lozère) respectively, which show high geographic variation for both characters. We conducted two different experiments to explore this issue. In the first one, hatchling lizards from the two populations were raised under identical laboratory conditions. This experiment showed that, when experiencing the same environmental conditions, the individuals of the two populations tended to grow at the same rate. This suggests that the observed differences in growth rate between geographically distant populations of *Lacerta vivipara* cannot be attributed to genetic factors, although we found evidence of within population genetic variability for growth rate.

In the second experiment, we raised hatchling lizards from one population (Lozère) in outdoor enclosures located in both sites (Brittany and Lozère). This experiment showed that transplanted lizards had both higher mortality and growth rate than lizards which stayed in their site of origin. These findings are in good agreement with the observed differences between the two natural populations. This experiment also showed that families with high survival and/or growth rate in one environment did not tend to have high survival and/or growth in the other environment, suggesting that genetic variation for plasticity of life history traits exists in the Lozère population.

Overall, our findings underline the potential role of phenotypic plasticity in explaining patterns of geographic variation of life-history traits, and that plasticity itself may be under genetic control.

Evolution of a generalist genotype: assessing the adaptiveness of phenotypic plasticity.

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Phenotypic plasticity is the ability of a genotype to adopt different phenotypes in different environmental conditions. These phenotypic changes may or may not be adaptive. If adaptive, we refer to the changes as adaptive phenotypic plasticity. Although some multivariate approaches to the study of phenotypic plasticity have been developed, most attention has been paid to the univariate case, i.e., the reaction norm. The goal of this work is to examine multivariate phenotypic plasticity to determine which characters are exhibiting adaptive phenotypic plasticity while controlling for phenotypic correlations

The focus is the inducible defense system involving the predaceous dipteran *Chaoborus* and the freshwater crustacean *Daphnia*. In the presence of *Chaoborus*, *Daphnia* adopt an alternative phenotype manifested by changes in many morphological characters. The induced phenotype is less vulnerable to predation by *Chaoborus*. Although the most noticeable characteristic of the induced morph of *Daphnia* is the necktooth (a small series of spines along the dorsal margin of the head), essentially all morphological characters exhibit some difference between the two morphs. I will be discussing three alternative ways of assessing the direct adaptive plasticity of these individual morphological characters with respect to the selective agent that causes them, i.e., predation by *Chaoborus*. The alternative ways of approaching this question yield very different results.

The most appropriate approach involves two steps. First, the adaptiveness of change for each character must be established, while controlling for phenotypic correlations. This can be estimated as the selection gradient, the partial regression of relative fitness on phenotype. The data used are the mean values for each phenotypic character in each clone and morph, along with an estimate of relative fitness derived from predation experiments involving *Chaoborus*. Second, the average induced change is estimated for the population. The direct adaptive plasticity for a character is the product of the appropriate element of the selection gradient and the averaged induced change. This product represents the direct increase in relative fitness in an environment with *Chaoborus* predation obtained by exhibiting the average induced change in that character. Of 8 morphological characters measured, 7 exhibit highly significant induced change in the population, and 5 exhibit a significant partial regression on fitness, i.e., a non-zero element in the selection gradient. Analysis of the direct adaptive plasticity indicates that 4 characters have a significant effect, with the necktooth being the single most important, followed by fornix width (lateral extensions of the head shield), body length, and tailspine length.

Gene silencing and mating system evolution in polyploid hermaphrodites

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The evolution of mating systems continues to be extensively studied at both theoretical and empirical levels. In this endeavor, polyploids have received much less attention than diploids, despite their prevalence among vascular plants and their occurrence among many animal phyla. I have studied the consequences of gene silencing for reproductive isolation and mating system evolution in polyploid, self-fertile hermaphroditic animals and angiosperms, building on a recent model of speciation in polyploid ferns. Assuming disomic inheritance in an allotetraploid, one or the other of the duplicated loci may fix deleterious or 'null' alleles, as long as the second locus remains fully functional. Patterns of silencing are likely to be different in independently evolving lineages: two populations may have the genotypes $aa\ 00$ and $00\ bb$ at a given locus pair, where a and b denote functional alleles, i.e., they are reciprocally silenced. Interpopulational 'hybrids' between such genotypes would be $a0\ b0$, and are thus expected to segregate for null alleles. Assuming that there is no gametic selection and that null alleles are fully recessive, it follows that 1/16 of selfed progeny will be homozygous for null alleles at both diploid loci. Outcrossing among reciprocally silenced genotypes thus involves the cost of partial hybrid sterility, and gene silencing can be regarded as an additional factor promoting self-fertilization.

However, it also follows that the magnitude of fitness loss depends on both the mating system of hybrids and on their relative proportion in local populations, in that high frequencies of hybrids and/or high selfing rates promote their sterility. One important prediction emerging from this scenario is that once such hybrids are generated, they should experience strong selection for outcrossing. This may be viewed as a special case of inbreeding depression, as previously masked deleterious alleles can suddenly be expressed in the progeny of these hybrids. The consequences of gene silencing for mating system evolution thus appear to be context-dependent.

The model-specific prediction of higher outcrossing rates in interstrain hybrids is currently being tested in genetically diverse populations of *Ancylus fluviatilis*, an allotetraploid freshwater pulmonate that has undergone some gene silencing subsequent to polyploidization. Previous work has suggested the preponderance of self-fertilization in this snail. Using progeny arrays from a large number of families and multilocus allozyme data (parent-offspring comparisons), the aim is to estimate outcrossing rates at the family and group levels ('pure strains' versus 'hybrids'). The first such data strengthen the previous inference of generally high selfing rates, but show higher outcrossing in some families, and should eventually reveal whether gene silencing has affected the mating system of hybrid snails.

Phylogenetic relationship of the European *Ips* bark beetles
(Coleoptera, Scolytidae): a mitochondrial DNA and allozyme analysis

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Ips acuminatus and *I. sexdentatus* infesting *Pinus silvestris*, *I. mansfeldi* infesting *Pinus nigra*, *I. amitinus*, *I. duplicatus* and *I. typographus* infesting *Picea abies* and *I. cembrae* infesting *Larix decidua* belong to the genus *Ips* De Geer (1775). A phylogeny of these seven species was derived from sequence and allozyme data to hypothesise the evolutionary divergence of their host relationship. The species are important pests in the European coniferous forests. Larvae and adults bore through the phloem layer disrupting the water flow and assimilate transport between roots and crown. In doing so they can kill even healthy looking tree stands during mass outbreaks, causing economic damage.

We examined divergence of the mitochondrial DNA by sequencing a COI region and further by analysing 5 polymorphic enzyme loci. The differentiation of the sequences based on about 600 base pairs was between 15% and 20% among species. The species were not clustered accordingly to the host tree e.g. *I. amitinus* and *I. typographus*, which are morphological quite similar, were grouped more distantly than e.g. *I. amitinus* and *I. acuminatus*. Even the scolytid outgroup *Blastophagus minor* had on average 25% divergence to the *Ips* species. Thus phylogenetic relationships of the mitochondrial haplotypes directly contradict hypotheses of species relationships from previous studies based on morphology and ecology. This high variation among species suggests that the species divergence is more ancient than previously thought and that genera were possibly grouped due to convergent morphological and behavioural evolution. However, the allozyme data revealed a contrasting relationship pattern. No loci fixed for alternate alleles was detected in the 5 loci comprising more than 50 alleles and the dendrogram was based on differences in allele frequencies.

The sequence divergence within the species was between 0% (e.g. *I. typographus*) and 3% (e.g. *I. cembrae*) whereas variation based on allozymes within single *Ips* sp. populations was high. The possible causative factors for this difference between the nuclear polymorphism and the low mitochondrial divergence within the species, including high gene flow and/or the occurrence of cytoplasmic incompatibility inducing *Wolbachia*, are discussed.

The rate of evolution of an induced life history response

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The evolution and ecology of inducible defences are rapidly growing fields. Inducible defences should evolve when there is a reliable cue to the presence of the selection pressure, when that selection pressure varies in space or time, and when defense is costly. These costs are expressed in life history traits: reduced growth and reproduction. Changes in life-history traits can be induced by environmental cues that are reliably associated with differences in age- or size-specific mortality rates. How fast can inducible life history responses evolve? In a long-term selection we are selecting 4 types of flies. Those in the first treatment (HAM) encounter high adult mortality and should evolve faster development, smaller size at eclosion, higher weight-specific fecundity early in life, and a shorter reproductive life, in approximately that order. Those in the second treatment (LAM) encounter low adult mortality and should evolve slower development, larger size at eclosion, lower weight-specific fecundity early in life, and a longer reproductive life. The flies in the third treatment (HAMP) encounter high adult mortality when propyl acetate (PA) is present (one month) in the larval medium and low adult mortality rates when it is not (the next month, in alternating sequence). They should evolve a plastic response to the environmental cue, PA, expressing the HAM phenotype when PA is present in their larval medium and the LAM phenotype when it is not. The flies in the second treatment (LAMP) experience the reverse: low adult mortality when PA is present and high adult mortality when it is not. They should express the LAM phenotype when PA is present and the HAM phenotype when it is not. Propyl acetate is nearly physiologically neutral, and larvae are attracted to it. We use it as an environmental cue to demographic conditions. These experiments bear on several important issues. Here we report on the rate of evolution of induced responses to PA as a cue to demographic conditions, using data from the HAMP and LAMP treatments.

Epistasis and the Evolution of Compensatory Fitness Mutations

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The analysis of epistatic interactions has played an important role in population genetic theory since it was introduced by Haldane and Wright. Historically, epistatic interactions are defined as interactions between genes. Epistatic interactions are expected to lead to nonrandom associations between polymorphisms at different loci within populations; however, nonrandom associations are rarely detected in natural populations. Most notably, extensive studies of linkage disequilibrium based on allozyme variation at many loci in natural populations of *Drosophila* have failed to lend support to Wright's ideas. In contrast, the observations emerging from the application of recombinant DNA technology to *Drosophila* population genetics show several examples of extensive nonrandom associations between DNA polymorphisms over relatively short distances. In the *Adh* and *white* locus regions of *Drosophila*, strong linkage disequilibria are clustered within the transcriptional unit.

We examined the hypothesis that the linkage disequilibria at *Adh* and *white* are caused by epistatic selection maintaining the secondary structures of messenger RNA in these regions. In its simplest form, the mechanism underlying the action of epistatic selection on secondary structure may be as follows: A mutation occurring in a secondary structural element such as the helix of an RNA hairpin may be individually deleterious because it increases the structure's free energy which may destabilize this structure. However, the pairing potential of a functionally important structure, and thus fitness, can be restored if a second "compensatory" mutation occurs in the complementary sequence of the helix. To examine this hypothesis, we first inferred RNA secondary structures in the regions of interest based on phylogenetic comparisons. Then, we tested the significance of the phylogenetically predicted stems using a newly developed likelihood ratio test and simulations. Our results suggest that the pattern of linkage disequilibria at *Adh* is consistent with this model of compensatory fitness interactions. The approximately 1-kb long "haplotype blocks" which we observed in a recent sequencing survey of *white* may be explained by a similar mechanism.

PHYLOGENETIC EVIDENCE THAT APHIDS, RATHER THAN PLANTS, DETERMINE GALL MORPHOLOGY

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Many diverse taxa have independently evolved the habit of living in plant galls. For all but some viral galls, it is unknown whether plants produce galls as a specialized plant reaction to certain types of herbivory or whether herbivores direct gall development. Here I present a phylogenetic analysis of gall-forming cerataphidine aphids that demonstrates that gall morphology is extremely conservative with respect to aphid phylogeny, but variable with respect to plant taxonomy. In addition, the phylogeny reveals at least three host plant switches where the aphids produce galls most similar to the galls of their closest relatives, rather than galls similar to the galls of aphids already present on the host plant. These results indicate that aphids determine the details of gall morphology, essentially extending their phenotype to include plant material. Based on this and other evidence, I suggest that the aphids and other galling insects manipulate latent plant developmental programs to produce modified atavistic plant morphologies rather than create new forms *de novo*.

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**Genetic variation in populations of the blowfly *Lucilia sericata*:
mitochondrial DNA sequences and Random Amplified
Polymorphic DNA analysis (RAPD).**

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The blowfly *Lucilia sericata* is a primary agent of cutaneous myiasis, largely affecting sheep. Although originally northern European in distribution, it has been spread worldwide with the global movement of domestic livestock. For this study, flies were collected from Britain, mainland Europe, North America, southern Africa, Hawaii and Australasia. Intraspecific genetic variation was studied by comparison of mitochondrial DNA (mtDNA) fragment sequences and random amplified polymorphic DNA (RAPD) analysis. A non-conserved mtDNA fragment was used, since its rapid rate of evolution is more appropriate to the study of genetic divergence between recently isolated populations; results from RAPD analysis formed the basis for a broad scale population study.

Phylogenetic methods (numerical and cladistic) were used to analyse the biochemical results. Further analysis of RAPD data using a recently developed randomization method to test for departures from random mating allowed the genetic homogeneity of *L. sericata* populations to be explored. Initial results highlight the existence of distinct patterns of global variation.

Accelerated rates of molecular evolution in the Blue Mussel, *Mytilus*

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Blue Mussels of the genus *Mytilus* have an unusual system of mitochondrial DNA (mtDNA) inheritance. Male mussels are heteroplasmic for two types of mtDNA. Although they receive mtDNA from both their mother and father, they only transmit their father's mtDNA and then, only to their sons. Females possess and transmit only their mother's mtDNA. This system has been dubbed "doubly uniparental inheritance" (DUI) of mtDNA and the class of molecules transmitted through males and females are referred to as the M and F types, respectively. A comparison of DNA and amino acid sequences for the mitochondrial genes *cytochrome c* oxidase subunits I and III for the M and F types from *Mytilus edulis* and *Mytilus trossulus* indicates that these sequences cluster together by gender rather than by species affiliation. In other words, the split between M and F types occurred prior to the divergence of these two mussel species. Another observation based on these data is that the M sequences are more divergent than the F sequences. On a broader taxonomic scale, it also appears that both *Mytilus* sequences (i.e., M and F types) evolve rapidly and are the most divergent mtDNA genomes yet observed. Specifically, our analysis of pairwise genetic distances between *Mytilus* M and F and ten other Metazoan sequences (representing mollusks, arthropods, deuterostomes and nematodes) indicates that the *Mytilus* comparisons are always the largest. Relative-rate tests (using *Drosophila* as a reference taxon) indicate that *Mytilus* has undergone a significant increase in its rate of molecular evolution within the Mollusca. Furthermore, by combining conservative estimates of times of divergence and branch lengths obtained from a neighbor-joining phylogenetic tree (based on a matrix of pairwise sequence divergence), the rate of molecular evolution (i.e., substitutions/site/lineage/million years) is faster in *Mytilus* than in either arthropods or vertebrates. We propose that the two unusual phenomena in *Mytilus* (i.e., DUI and a high rate of mtDNA sequence divergence) may be causally related. DUI involves a physical separation of the M and F types into sperm and eggs, and the M type (which is not present at all in females) is also the minority molecule in male somatic tissue. This separation into distinct environments could introduce different selection pressures on the M and F types and, perhaps, decrease the sum total selection pressure on either type. There is evidence from the sequence of these protein coding genes that the rate of nonsynonymous substitutions is higher in the M lineage than in the F lineage. If DUI does reduce selective pressures on one or both of these gender-associated lineages, and if the phenomenon of DUI is old and dynamic (appearing, disappearing, and re-appearing), it may explain the unusual rate of molecular evolution in these mussel sequences.

The causes and significance of Haldane's rule in the meadow grasshopper
Chorthippus parallelus

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Haldane's rule states that if only one sex is sterile or inviable among species' hybrids, it is the heterogametic sex. The causes and significance of this phenomenon are contentious issues, and this study aims to test some recently formulated ideas using the Pyrenean hybrid zone between subspecies of the meadow grasshopper, *Chorthippus parallelus parallelus* and *Chorthippus parallelus erythropus*, as a model system.

Laboratory-bred hybrid males of *Chorthippus parallelus* are subject to Haldane's rule, and are completely sterile, but no hybrid male sterility has yet been recorded in the field. Virdee & Hewitt (1994) have demonstrated an asymmetry in dysfunction among reciprocal crosses using natural hybrids, which implies the presence of modifiers for dysfunction. The initial component of this current study comprised the setting up of crosses between grasshoppers from corresponding sites at the Col du Pourtalet and the Col de la Quillane, in order to test for the existence of such modifiers, and to elucidate the spatial homogeneity of their genetic architecture. If different modifier genes have arisen across the geographic range it is predicted that crosses will lead to the breakdown of modification and hence dysfunction. Results from these crosses will be discussed.

Additionally, grasshoppers were sampled at 5km intervals along a transect through the Col de Bouchero, and a preliminary morphometric analysis performed on characters known to differ at the subspecies level. Clines for all characters are apparently exactly coincident and displaced 5km south of the zone centre, which implies introgression of the *C p parallelus* genome across the col into Spain. Crosses have revealed preferential inheritance of the *parallelus* X (Bella *et al.*, 1992), which may arise from a conflict between meiotic drive genes on the X chromosome and autosomal drive-modifiers. Further work will involve testing this hypothesis with crosses.

The sterile worker castes in social insects pose an evolutionary enigma: how can natural selection, a process based on propagating genes to the next generation, promote such altruism? Hamilton's rule and the concept of inclusive fitness provide a theoretical framework for understanding the evolution of altruism: individuals may gain reproductive success also through other relatives than own offspring. Especially in social hymenopterans kin selection appears to be a major factor favouring sociality, since the haplodiploid sex determining system causes females to be more closely related to sisters than to their own offspring. However, haplodiploidy also causes asymmetric genetic relationships within colonies: females are equally related to all offspring (males and females), but more closely related to sisters than to brothers (relatedness asymmetry). This, in combination with predictions from sex ratio theory, parent-offspring conflicts and kin selection theory, reveals a conflict between colony queens and workers over sex allocation. Workers maximise their inclusive fitness by producing a female biased sex ratio, whereas the colony queen maximises her fitness by a sex ratio closer to unity. Hence, inclusive fitness arguments provide a basis for predicting reproductive characteristics of social insect colonies and analysing the outcome of the worker-queen conflict. Conversely, sex allocation studies in social insects can be used to test inclusive fitness theory itself, since worker control over sex allocation is expected under kin selection. The most powerful such test is the analysis of individual colonies where the predicted sex allocation varies due to differences in worker fitness functions. Previous work has shown that in a number of species workers apparently are in control of the final sex ratios produced in their colony. However, queens can control the sex ratio of the eggs that are laid, since only fertilised diploid eggs develop into females whereas unfertilised, haploid eggs develop into males. Hence, to bias sex ratios in their favour workers must be able to selectively destroy male brood. This study presents empirical evidence of worker-controlled facultative sex ratio biasing in response to relatedness asymmetries caused by inter-colony variations in queen mating frequencies. Whether the workers change brood sex ratios can be analysed by comparing the primary (egg) sex ratio laid by the queen in spring with the secondary (final) sex ratios raised from the same cohort of brood. The results show that male eggs are selectively destroyed in colonies producing all female brood and that there is no association between the primary and secondary sex ratio. Hence, queens apparently have very little control of sex allocation in the species studied here (*Formica exsecta*).

Mate quality affects offspring sex ratio in the blue tit (*Parus caeruleus*). TE

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Questions concerning the occurrence of adaptive sex ratio manipulation have a long research tradition in evolutionary biology, but evidence from birds is scarce. It has been suggested that birds are unable to adaptively determine the sex of their young due to the constraints of their sex determination systems. Here we report results from a study of variation in nestling sex ratio in the blue tit (*Parus caeruleus*), a small passerine bird laying large clutch sizes. Using the technique of flow cytometry, which quantifies sexual differences in the total amount of DNA in blood cells, we determined the sex of 389 blue tit nestlings from 41 broods. The overall hatching sex ratio between broods was significantly greater than expected from a binomial distribution, suggesting that the nestling sex ratio does not simply reflect random chromosomal segregation at meiosis, but that females in some way can control the sex of their individual eggs. Brood sex ratios were not significantly affected by brood sizes or timing of breeding, in contrast to some previous studies. Nestling sex ratios of the broods were instead influenced by properties of the fathers: females mated to males that survived until the next breeding season (high-quality males) produced male-biased broods, as opposed to those that were mated to males that did not survive (low-quality males). Although it has previously been proposed that females should produce an excess of sons when mated to high-quality males, our data provide the first evidence that the father's phenotypic quality influences the sex ratio variation in a natural population.

Plumage condition affects flight performance in starlings: implications for developmental homeostasis, abrasion and moult. John P. Swaddle - *Behavioural Biology Group, School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, U.K.*

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Variation in length and asymmetry of wing primary feathers can arise from a breakdown of developmental homeostasis, feather abrasion and incomplete growth during moult. Indirect predictions have been made concerning the impact of primary length and asymmetry on the flight ability of birds, but they have not been explicitly tested. Here I provide evidence from both natural variation in primary feather condition and experimental manipulations of primary feather length and asymmetry to indicate that these factors do influence aspects of flight performance in the European starling (*Sturnus vulgaris*). Damaged and incompletely grown primary feathers reduce escape flight performance. Experimentally reduced primary lengths reduce the take-off speed; increased feather asymmetry decreases aerial manoeuvrability. A comparison of the experimental and natural plumage data indicates that birds in the wild may be able to adapt to their change in wing morphology, perhaps to minimise the effect of feather loss or damage on flight performance. The results from this study indicate that primary feathers are under strong stabilising selection to maximise developmental homeostasis and reduce feather asymmetry. These findings are also of ecological importance to the damage-avoidance and moult strategies of these birds. This is the first experimental evidence to indicate a quantitative reduction in flight performance with feather lengths and asymmetries typical of those observed during flight feather moult and feather damage in any species.

SELFISHNESS AND THE INTEGRATION OF GENETIC INFORMATION DURING EVOLUTIONARY TRANSITIONS

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It has happened a number of times in evolution that originally unlinked replicators have formed a higher-level unit: unlinked genes have been engulfed in compartments, genes have been linked into chromosomes, and organelles have joined eukaryotic host cells. The question naturally arises how mechanisms to prevent unbounded competition of the lower-level replicators evolved. Contemporary analogues can also be pointed out. It seems that some form of population structure was essential for cooperation to arise. Three of them will be discussed in some detail:

- 1) Structured demes. Selection in them explains the dynamics of defective interfering viruses and the existence of coviruses (segmented multi-compartment viruses).
- 2) Replication and diffusion on surfaces, as modelled by cellular automata. Coexistence of complementing, but competing replicators can arise either through some mesoscopic structure (hypercyclic spiral waves) or without an obvious pattern (metabolic co-operation). The general importance of this mechanism will especially be emphasized.
- 3) The stochastic corrector model: group selection of reproducing compartments. This model is applicable to the gene ---> protocell transition, to the establishment of chromosomes in protocells, to the coexistence of different plasmids under selective conditions, to the nuclea dynamics of hypotrich ciliates, and to the archezoan ---> metakaryote transition (coexistence of semi-autonomously replicating organelles).

Population genetic structure of *Pinus sylvestris* (L.) revealed by analysis of allozyme and RAPD variation: discrepancies and similarities.

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Abstract

Several recent studies have compared the usefulness of allozyme and random polymorphic DNA (RAPD) markers for population genetic analysis of plants. In most of these studies, only diploid material was studied. In such material, heterozygotes cannot be distinguished from dominant homozygotes because of the dominant nature of RAPD variation. In conifers, this limitation can be alleviated by using haploid macrogametophytes which permits determination of allelic composition of any individual for a given locus. We analysed allozyme and RAPD variation in haploid macrogametophytes of forty single trees in two populations of *Pinus sylvestris* (L.). RAPDs showed higher expected and observed heterozygosity than did allozymes. The genetic distance between the two investigated populations was low and similar for allozyme and RAPD loci. In both populations, fixation indices (F) were high and negative for all RAPD loci, indicating heterozygote excess over the expected panmictic proportions. In contrast, both positive and negative F values were observed among allozyme loci with an average showing only modest departure from panmictic expectations. Several hypotheses are proposed to explain the observed discrepancy between F values for allozyme and RAPD loci.

356 The Maintenance of Alternative Phenotypes by
Threshold Selection, Mutation and Drift

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The evolutionary maintenance of alternative phenotypes by mutation, directional selection and genetic drift is analysed by a diffusion approximation of gene frequency distribution and a Monte Carlo simulation. The alternative phenotypes (a dichotomous character) are assumed to be determined by the threshold model of quantitative genetics. We assume an ideal truncation selection against one of the phenotypes: all individuals of one morph (individuals in which the underlying character is lower than the threshold point) do not reproduce at all. This scheme of selection is quite different from the usual truncation selection, where the truncation point moves with evolutionary changes of the genotypic distribution and the directional selection intensity is kept constant. At equilibrium substantial amounts of additive genetic variance can be maintained in the population. The proportion of the unselected phenotype is mostly determined by the per-locus (not genomic) mutation rate in a large population. In a small population (population size < 1000), however, the number of individuals with the unselected phenotype is nearly independent of the per-locus mutation rate, the number of loci and population size. The result implies that one individual with the unselected phenotype appears every two or three generations in a small population. Thus, mutation and drift can maintain alternative phenotypes even in a small population.

Rules & Mechanisms in the Evolution of Foraging Behaviour

Recently there has been renewed interest in proximal mechanisms in behavioural ecology. Laboratory studies with bumble bees (*Bombus* spp.) were designed to elucidate the mechanism by which bees decide to depart patches. Captive bees foraged from rings of 3 wells drilled in blocks of Plexiglas; the rings were filled with from 0-4 μL 30 % sucrose solution and were designed to mimic flowers borne in umbels. In tests with pairs of rings, bees probed 2 wells on average before departing when encountering an empty ring, and they probed 10 wells on average when first encountering a filled ring. Receiving sucrose from one ring had a consistent carryover effect: bees probed an average of over 3 wells before departing on empty rings if they had first visited a filled ring. Further tests used triangles of rings and varied amounts of sucrose solution in the wells. Bees probed fewer wells on both 1 μL rings and 4 μL rings than on those with 2 μL . In both 2 and 4 μL triangles, the numbers of wells probed declined from first to third rings. When visiting empty rings, the number of wells probed before departure depended on previous experience: bees always probed more wells on empties if they had first visited one or two filled rings, and the effect varied with nectar volume. Effects of filled rings were asymmetric: bees probed more wells on empty rings after first visiting a 2 μL and then a 1 μL ring than vice versa. To explain the results I present a model based on an increment-decay mechanism. I discuss the difference between "rules" vs. mechanisms as proximal models of foraging behavior.

Phenotypic plasticity in *Iris pumila* - spatial and temporal aspects

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T11

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I conducted an exploratory analysis of the phenotypic plasticity in dwarf bearded iris - *Iris pumila* L. (Iridaceae). *I. pumila*, rhizomatous perennial insect-pollinated herb, is very suitable object for studies of phenotypic plasticity for several reasons. First, since it can reproduce vegetatively, parts of the same clone can be grown in different environments (spatial aspect of phenotypic plasticity). Second, due to its perennity, clones of *I. pumila* can be monitored in different years (temporal aspect of plasticity).

22 quantitative traits were measured on parts of clones from two populations (Brdačce and Borova šumica - 30 clones each) transplanted on experimental plots in "Brdačce" and "Borova šumica" localities. Each clone was represented by two replicas and monitored in three flowering seasons (1992, 1993 and 1994). Collected data was analyzed in several ways by SAS (SAS Institute 1989) statistical package. On the basis of results of performed analysis, I had come to following conclusions:

1) *Analyzed traits exhibit phenotypic plasticity in face of both spatial and temporal environmental variabilities.* This was indicated by treatment effects in two-way and repeated measures ANOVA's.

2) *Genetic variability of phenotypic plasticity is considerably low for most of the analyzed traits.* Evidence for such conclusion can be found in small number of significant interaction terms in two - way and repeated measures ANOVA's. Low genetic variability indicates small potential of phenotypic plasticity for changes by selection.

3) *Phenotypic plasticities of the same trait were similar in different populations for most of the analyzed traits.* This conclusion is based on the lack of significant interaction terms (population x locality and population x year) from two - way ANOVA's. Possible explanations for this similarity are lack of genetic variability of phenotypic plasticity and/or similarity of "selection regimes" in different populations.

4) *Traits divergence between populations was not followed by divergence of plasticities.* Changes of trait means should be followed by changes in trait's phenotypic plasticity under the expectations of so-called "pleiotropic model" ¹. Observed lack of correlation between trait and trait's plasticity divergences is in better agreement with "epistatic model" ¹ of plasticity's genetic determination.

5) *Traits with high phenotypic plasticity do not diverge less.* It is often assumed that high phenotypic plasticity should act as a "buffer against selection" ^{2,3}. Divergence between populations for trait means was not prevented by high phenotypic plasticity in case of *Iris pumila*.

6) *Phenotypic plasticity and genetic variability of the same trait were positively correlated.* Some authors state: that phenotypic plasticity and genetic variability are alternative ways of adaptation to heterogeneous environments. My results are in better agreement with expectations that phenotypic plasticity and genetic variability can be positively correlated ⁴ because they are adaptations to the same factor (heterogeneity of environment).

7) *Phenotypic plasticity and developmental instability do not have common genetic basis, at least for the most plastic, vegetative traits.* Such conclusion can be drawn from lack of any significant correlation coefficients between measures of phenotypic plasticity (variability between years and between localities) and instability (asymmetry, variabilities between ramets and between replicas of the same clone) for vegetative traits. For floral traits significant correlations were detected but only for variability between years (as a measure of phenotypic plasticity) and variability between different replicas in the same environment (as a measure of instability). This measure of instability can also be a result of plastic response to uncontrolled environmental variation ⁵ and, therefore, observed positive correlation can reflect positive relationship between different phenotypic plasticities of floral traits.

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ITS polymorphisms and their meaning for concerted evolution
in *Drosophila melanogaster*

IT 2

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The internal transcribed spacer (ITS) is part of the ribosomal rDNA cluster. Interspecies comparisons have shown that a large portion of the ITS is evolving neutrally. Therefore, the ITS provides a useful marker to monitor genetic exchanges driving concerted evolution.

In *Drosophila melanogaster* ribosomal genes are located on the X and Y chromosome. Concerted evolution of the rDNA arrays is dependent on genetic exchange between the X and Y chromosome. We found three different levels of genetic exchange to be involved in homogenization of the rDNA clusters: within single chromosomal lineages, between homologous chromosomes and between non homologous chromosomes. Comparisons of ITS polymorphisms within natural populations suggest that these exchanges have very different rates. Intrachromosomal exchange is the most frequent exchange mechanism, leading to the predominance of homogenized rDNA arrays on single chromosomes. However, genetic exchange between homologous chromosomes is still frequent enough to detect "composite" rDNA arrays. Genetic exchange between rDNA clusters on the X and the Y chromosome are apparently significantly less frequent.

Hamilton and Zuk theory suggests that male 'brightness' allows females to assess male ability to resist parasites. In this hypothesis the full expression of secondary sexual traits and parasite load are respectively assumed to mainly depend on individual vigour and genetic resistance. Here, we propose that a negative correlation between brightness and parasite load incorrectly suggest a causal relationship between parasitism and mating success. Indeed, parasitism can negatively covaries with host age in certain circumstances of host mortality induced by parasite accumulation, while both male brightness and female preferences positively covaries with age. Thus some properties of host-parasites associations, coupled with the host reproductive behaviour can provide fortuitously supports for the Hamilton-Zuk hypothesis.

Parasites, age and sexual selection

LONG-TERM PARTHENOGENESIS AND THE EVOLUTION OF
ACARIFORM MITESRICHARD H. THOMAS¹ & ROY A. NORTON²¹Department of Zoology, The Natural History Museum, Cromwell Road,
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We are studying a higher taxon of oribatid mites, known colloquially as the nothroids, which appears to have dispensed with sex altogether, yet contains hundreds of species that are numerically abundant, geographically widespread and geologically old. This situation is precisely the opposite of typical parthenogenetic species which are relatively very young and invariably have sexual sister species. Intensive and extensive sampling of natural populations of many nothroid species provides no evidence for geographic parthenogenesis or for cyclical parthenogenesis, thus any sexual reproduction in these animals must be occurring at extremely low frequency. Fossil evidence places the origin of these lineages in the Devonian, over 380 Mya. The most parsimonious interpretation of the available data is that these animals have speciated and diversified in the absence of sex. Morphological evidence suggests that a major group of acariform mites, the Astigmata, has evolved from within the asexual nothroids. The Astigmata is a very diverse group containing, among others, house dust mites, stored products pests, parasites, and slime mites (of *Drosophila* culture fame). Parthenogenesis occurs only sporadically throughout this group, as in most invertebrate groups. We present results from DNA sequence data testing the monophyly of the asexual nothroid lineages and investigating the origins of the Astigmata.

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Fluctuating Asymmetry and Honest Signaling of Phenotypic Quality in Human Sexual Selection.

Judgments of facial attractiveness are expressions of psychological adaptations, presumably for mating. Thus, the form that sexual selection took in the evolutionary history of humans is knowable from the judgments. Four models of the sexual selection process have been proposed to account for the evolution of secondary sexual traits: arbitrary or aesthetic model, the good genes model, the mate recognition model, and the good provider model. Degree of symmetry reflects the degree of developmental health, and probably overall phenotypic quality. The arbitrary and mate recognition models predict a positive correlation between facial asymmetry and the sex-specific development of attractive facial secondary sexual traits. The good genes and good provider models predict a negative relationship between the same variables. A negative relationship was found. This research provides evidence, then, that secondary sexual features of the face honestly signal phenotypic quality. Other research reveals that non-facial secondary sexual traits of men also signal phenotypic quality. The research discussed was done in collaboration with Steven W. Gangestad.

**Introgression of mitochondrial DNA between two hare species
in Scandinavia.**

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In Scandinavia two species of hare occur, the European hare (*Lepus europeus* Pall.) and the mountain hare (*L. timidus* L.). The European hare has been introduced since the 19th century. The two species are known to hybridize and produce viable offspring in captivity. Morphological intermediates, believed to be hybrids, have been observed in the wild. Analysis of mitochondrial DNA restriction fragment length polymorphism (RFLP) was performed to investigate whether hybridization between the two hare species occur in the wild. Morphologically distinct specimens of European and mountain hares were collected from totally 15 localities in Scandinavia. The sequence divergence in mtDNA between the species was estimated at 8%. Intraspecific mtDNA sequence divergence varied between 0.09-0.4% in European hares and 0.1-1.4% in mountain hares. Six out of eighteen European hares examined carried mtDNA of mountain hare origin. No mountain hare with European hare mtDNA was found. Thus, our study demonstrate introgression of mtDNA haplotypes from mountain hares to European hares. The results indicate that interspecific hybridization between wild female mountain hares and male European hares occur and that the hybrids are fertile.

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T8

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Some thoughts about the origins of syntax

Teaching experiments with a pygmy chimpanzee seem to show that this animal has some grammatical skill since he comprehends and creates meaningful differences given between alternative word orders.

What is the significance of this finding? Is the bonobo's performance an evolutionary precursor for the grammar, or may this capacity be of interest but have no significance from an evolutionary point of view?

A unique dissolution occurring in human speakers i.e. morpheme use impairment with intact syntax throws a new light upon this question. This finding raises the possibility that the present day unitary grammatical system has different evolutionary roots which reflect different time and context.

The syntax i.e. the combination of linguistic elements for creating different meanings might have originated earlier in the hominoid evolution, while using morphemes to join elements is presumably a recently evolved capacity. The syntax (in this meaning) serves as a precondition for the arising morphological system, but the true grammar with its special evolving is present only when the latter is established.

SEX RATIO AND NATURAL SELECTION IN HUMANS: INTER- AND INTRA-
POPULATION ANALYSES.

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P16

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In humans the secondary sex ratio (males/females at birth) exceeds, slightly but significantly, the expected 1:1 segregational ratio. It is well known, however, that sex ratio values varies over lifetime: since mortality rate is higher in males than in females at most ages, sex ratio is progressively reducing so that at the reproductive age it is closer to 1, this value being very likely stabilized by natural selection. Secondary sex ratio can show variations between and within populations, and its temporal trend follows different patterns in different populations. Both genetical and environmental factors have been invoked to explain *interpopulation* variability, whereas biological and socio-economic variables, such as parity, parental age and social class, are generally considered to play a primary role in determining *intrapopulation* variability.

In previous papers we studied with different approaches the above mentioned causes of the sex ratio variability. We considered large populations representative of the main human groups and we compared the secular trends of the sex ratio. The data covered a period of over fifty years. In the Italian population, furthermore, we analyzed the covariation of secondary sex ratio with some biological and socio-economic parameters.

In the present work we summarize the main results of these studies and we report a preliminary analysis performed on different Italian regions which are at different stages of demographic transition. We have studied a partitioning of the sex ratio variability: in an attempt to isolate any specific effect, we have used a statistical multivariate approach to analyze the relationships between sex ratio and relevant socio-economic and biological parameters, such as stillbirth rate, parity and maternal age and educational level.

Ulizzi L. (1983) *Ann.Hum.Genet.*, 47:321-327; Ulizzi L. and Zonta L.A. (1993) *Ann.Hum.Genet.*, 57:211-219; Ulizzi L. and Zonta L.A. (1994) *Hum. Biol.*, 66:1037-1048; Ulizzi L. and Zonta L.A. (1995) *Hum. Biol.*, 67:59-87

PLASTICITY IN REPRODUCTIVE TACTICS IN A FRESHWATER COLONIAL ANIMAL

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P11

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Life-cycles of modular, colonial animals involve both asexual reproduction and sex. In the generally sessile life-style of modular organisms, different forms of growth and reproduction function both in local foraging for resources and spatial and temporal dispersal. In different environments, partition of resources among the reproductive functions can be expected to vary.

We studied the reproductive tactics of Cristatella mucedo (BRYOZOA: Phylactolaemata) in different experimental conditions in two different flow regimes and standing water. The conditions affected the pattern of water flow over the substrata, and probably also the availability of food. Reproductive traits studied were: clonal growth of colonies by budding of daughter zooids, fission of colonies, production of asexual resting stages (statoblasts), and production of sexual larvae.

Rearing conditions clearly affected clonal growth, but the performance of colonies of different origin (colonies collected from separate sampling locations) ranked differently between the conditions. The effect of colony origin on sexual reproduction and initiation of statoblast production was more pronounced than that of the growth conditions. In general, there was a positive correlation between the different reproductive traits.

The results suggest a rapid phenotypic response to different growth conditions in clonal growth of Cristatella colonies. Production of statoblasts and larvae, in turn, may be better buffered against environmental changes. The observed patterns in responses may be due to differences in reaction norms among genetic individuals. Because of the strong effect of origin of colonies, we conclude that reproductive tactics may differ among populations.

ACCESS TO MUSEUM COLLECTIONS FOR EVOLUTIONARY STUDIES
Extraction, amplification and sequencing of DNA from unbuffered
formalin-fixed specimens

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P7

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Museum collections around the world contain many millions of specimens fixed in unbuffered formaldehyde and preserved in ethanol. A large number of these wet specimens were obtained at great expense from remote parts of the globe and would be difficult or impossible to recollect. The use of fixed specimens for evolutionary studies based on molecular markers is of great interest because it significantly widens the number of taxa which can be used for phylogeny and/or population genetics. Recent focus on rare or extinct species exacerbates this relevance.

Recent advances in the technology of DNA analysis have allowed some museum collections to become valuable sources of DNA. However, organisms which are stored in liquid preservatives have been used less in molecular biological studies than dried skins or ancient bones, as evidenced by the relative lack of publications on this subject.

Our work is devoted to the use of unbuffered formaldehyde fixed museum specimens as a source of DNA. After having analysed the effects of this common fixative on DNA we set up a protocol suitable for the recovery of DNA from formaldehyde fixed specimens. DNA extracted following our protocol can be amplified (up to 500 bp) and sequenced. Examples are given using frog specimens.

We also report a study, the aim of which is to define a new recipe for liquid fixatives that will preserve both whole animal morphology and DNA.

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GENETIC VARIATION IN THE STANDS OF ENGLISH OAK (*Quercus robur*) AND EUROPEAN WHITE ELM (*Ulmus laevis*) IN FINLAND.

The Finnish populations of *Quercus robur* and *Ulmus laevis* represent the northern margin of both species' distribution in Europe. The natural occurrence of *Q. robur* is restricted to the SW-corner of Finland; *U. laevis* is found on the shores of a lake area in the central Finland and in a few isolated stands elsewhere. Both species have undergone a decline in the past, first due to the change in the climate over a period of thousands of years and then a rapid one due to the human activities. The processes resulted also in a fragmented distribution pattern. *U. laevis* is regarded as a threatened species in Finland.

Genetic variation of the stands was analyzed electrophoretically for 13 enzyme loci in *Q. robur* and for 20 loci in the case of *U. laevis*. The observed heterozygosity is quite low in the stands of *U. laevis* when compared to other broadleaved trees. The genetic variation in the stands of *Q. robur* is slightly below that of German stands. The genetic differentiation of the adult oaks is at the same level with the central European populations, but seems to be increasing at the juvenile stage.

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P4

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INDUSTRIAL MELANISM OF MOTHS IN FINLAND

Industrial melanism of moths has been monitored in Finland over 20 years starting in 1972. Melanic forms have been observed in more than 40 species (northern melanism excluded), but in most cases only sporadically. Most important species are two small noctuid moths, *Oligia latruncula* and *Oligia strigilis*, followed by *Apatele rumicis*, *Tethea or* and *Ectropis crepuscularia/bistortata*. Only a few melanic Peppered moths have been recorded.

The frequency of melanics of *O.latruncula* ranges from 0.8 to 1 in all urban populations. The melanism of *O.strigilis* is restricted to 3-4 towns and the frequency of melanics is always below that of the other species. High melanic frequencies have been recorded also in rural populations of *O.latruncula* in the SE-part of the country and in the southern archipelago, whereas rural melanism of *O.strigilis* is very uncommon.

Temporal changes in the melanic frequencies are mostly alarming: there is a slight decline in the case of *O.latruncula* in the center of Helsinki, but a rapid increase in the rural populations over large areas. These changes and some details of the geographic pattern are not connected to lichen damage and thus, selective predation is probably not the only selection component.

Non-equilibrium Population Dynamics of 'Ideal and Free' Prey and Predators

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T10

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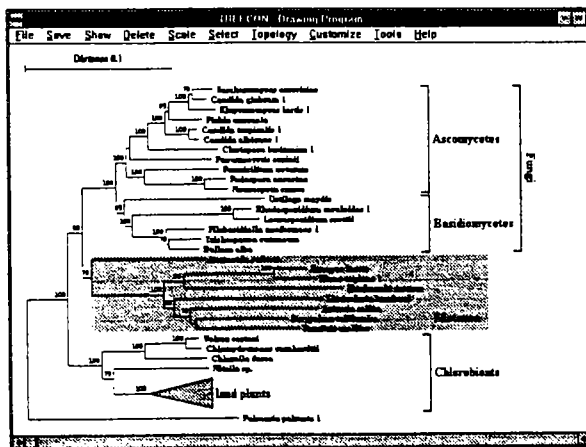
It is long known that aggregated spatial distributions of prey and predator may promote ecological stability (i.e., stability of the population dynamical equilibrium). However, ideal free prey and predators will settle at sufficiently aggregated distributions only if patch quality (reflected in prey fecundity) is very heterogeneous. Hence, the conditions for simultaneous ecological and evolutionary stability are rather limited. We present the results of a systematic survey using computer simulations, suggesting that adaptive patch choice may lead to non-equilibrium persistence under a much wider range of conditions, depending on the way the ideal free distributions are achieved and, in particular, on the information that is available. If prey and predators can distinguish among patch types but cannot detect population densities within the patches, spatial distributions will be density-independent. Then, parameter space contains a region of ecological stability that is surrounded by a region of limit cycles. If predators or prey can detect population densities within the patches, they can adopt flexible patch selection strategies. Spatial distributions become density-dependent, and the set of inhabited patches is no longer constant; ideal free distributions will expand and shrink when populations fluctuate. If only the predators can adopt flexible patch selection strategies, the equilibrium becomes unstable and ecological stability vanishes. Nevertheless, predator and prey may coexist in a limit cycle if there are enough marginal patches, and prey fecundity in the high-quality patch is sufficiently large. Thus, a flexible aggregative response of the predators is a destabilizing mechanism, that nonetheless may contribute to persistence. If both prey and predators have flexible patch selection strategies, simulations lead either to chaotic fluctuations or to extinction, but not to stable equilibria or limit cycles. The conditions for coexistence by far exceed those for ecological and evolutionary stability when distributions are density-independent.

TREECON for Windows: a software package for the construction and drawing of evolutionary trees for the Microsoft Windows environment

P7

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TREECON is a software package developed primarily for the construction and drawing of evolutionary trees based on distance data calculated from nucleic and amino acid sequences. It implements several equations for converting dissimilarity into evolutionary distance and several algorithms for inferring tree topologies. Bootstrap analysis on sequence data is also implemented. The software package, which was initially developed to run under the DOS operating system, has now been adapted for the Microsoft Windows environment. TREECON for Windows has a standard MS-Windows interface including pull-down and pop-up menus, dialog boxes and scrollable lists. It is therefore assumed that users are familiar with the basic interface elements of MS-Windows. TREECON for Windows is written in C and runs on IBM-compatible computers (80386 and higher). A hard disk and a mouse are required. The software package consists of several executables which are managed through a principal menu. As dynamic memory allocation is used throughout the program, the size of the data is constrained only by the available memory. Trees as shown on the display (see figure) can be scrolled in both directions and customized to the needs of the user. The user can select different colors and different fonts for species names, bootstrap values, cluster names and so on. Furthermore, selected numbers of species can be put in different fonts and clusters of sequences can be represented as triangles or by shading. Taxon designations can also be added. Trees can be saved in different formats (text, HPGL, ...) and printed as they appear on the screen (WYSIWYG). On-line help is also available. TREECON for Windows is available from the authors for a minimal fee to defray the costs of diskettes and mailing. Please contact the authors for details by email at yvdp@uia.ua.ac.be or dwachter@uia.ua.ac.be.



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The evolution of stramenopiles and alveolates based on small ribosomal subunit RNA taking into account nucleotide variability

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One of the characteristics of the small ribosomal subunit RNA (SSU rRNA) is that conservative areas of the molecule are interspersed with areas of variable structure. In the course of evolution, the latter areas accumulate substitutions, insertions and deletions at a much higher rate than the more conservative ones. This structural organization permits the study of phylogenetic relationships over a wide spectrum of phylogenetic distances. However, a substitution in a variable area of the molecule does not have the same phylogenetic meaning as a substitution in a more conserved area of the molecule. Most evolutionary studies do not take into account this distinction. In some studies all nucleotides are treated equally, in others, variable areas are completely excluded from the analysis, under the pretext that they can not be dependably aligned.

As we have put some effort in the unravelling of local secondary structure models for the most variable areas, for which evidence can be found by the observation of compensating substitutions in the sequence alignment, we feel that they can be aligned with sufficient confidence to be included in phylogenetic analyses. However, since variable areas fix mutations at a much higher rate than conservative ones, a correction should be applied which is function of the variability of the area considered. The variability of a position can be defined as a quantity proportional to its rate of substitution during evolution. When the substitution rate for each position is known, all SSU rRNA sequence positions can be divided into a number of sets, each set consisting of positions of comparable variability, i.e. fixing mutations at a similar rate. Once the alignment has thus been calibrated, a new distance matrix can be computed, based on a specific correction for each subset of positions. This 'substitution rate calibration' has been applied to the evolution of stramenopiles and alveolates.

The stramenopiles comprise species that either possess evenly spaced tripartite tubular hairs attached to the flagellum or other parts of the cell surface, or species that have been derived from organisms having these structures. Taxa presently included in the stramenopiles are the bicosoecids, labyrinthuloids, oomycetes, hyphochytriomycetes, diatoms, chrysophytes, phaeophytes, xanthophytes, and eustigmatophytes. Alveolates comprise the ciliates, dinoflagellates, foraminifers, and apicomplexans, and are characterized by the possession of alveoli, which are membrane-bound flattened vesicles or sacs underlying the plasma membrane. Phylogenetic reconstructions based on SSU rRNA regularly suggest stramenopiles and alveolates to be sister although bootstrap support for this grouping is usually low.

Tree topologies based on 'substitution rate calibration' do not suffer from anomalies caused by the presence of extremely long branches. Furthermore, since the method makes it possible to use the complete sequence alignment, even when distantly related organisms are included, trees are not dependent on the choice of the alignment region used.

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The relationship between latitudinal clines and life history traits
in *Drosophila melanogaster*

T4

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Latitudinal clines are found on both hemispheres for the allozyme loci alcohol dehydrogenase (*Adh*) and α -glycerophosphate dehydrogenase (α -Gpdh), for the inversion *In(2L)t* and for quantitative traits like body size and thermal resistance. The relationships between these characters and their adaptative significance will be discussed.

The phylogeny of the mastigomycetes as inferred^P from large ribosomal subunit rRNA sequences

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Zoosporic fungi are lower fungi that produce motile reproductive cells bearing one or two flagella. Three of these fungi, viz. chytridiomycetes, oomycetes and hyphochytridiomycetes have been classified in the past as mastigomycetes, and they are distinguished on the basis of the number and type of flagella present on the zoospores. Hyphochytridiomycete zoospores have one flagellum, which is directed anteriorly during motion and bears flagellar hairs or mastigonemes. Because of the mastigoneme action, the cell is pulled by the flagellum. Chytridiomycetes produce zoospores that also have a single flagellum, but it does not have mastigonemes. It is directed posteriorly and pushes the cell forward. The zoospores of oomycetes have one flagellum of each kind.

On the basis of small subunit ribosomal RNA (SSU rRNA) sequences, it was already shown that the mastigomycete grouping is an artificial one: the chytridiomycetes cluster with the zygomycetes and higher fungi, while the oomycetes cluster with the heterokont algae, an assemblage referred to as the stramenopiles. The heterokont algal group consists mainly of the chrysophytes, eustigmatophytes, xanthophytes, bacillariophytes and phaeophytes. We determined the SSU rRNA sequence of the hyphochytridiomycete *Hyphochytrium catenoides*, and as was expected on the basis of biochemical and ultrastructural data, this sequence also clustered with the stramenopiles.

We also determined the large subunit ribosomal RNA (LSU rRNA) sequences of the oomycete *Phytophthora megasperma*, the chytridiomycete *Blastocladiella emersonii* and the hyphochytridiomycete *Hyphochytrium catenoides*. Phylogenetic trees based on LSU rRNA confirm that the mastigomycetes are at least diphyletic. Preliminary results indicate that *B. emersonii* diverges first in the fungal clade, before the zygomycetes and the higher fungi. *P. megasperma* and *H. catenoides* cluster together, but no other stramenopile LSU rRNA sequences are known yet. In the future, some heterokont algal sequences will be determined in order to further investigate the relationships within the stramenopiles, which still remain controversial. The relationships of the stramenopiles and true fungi relative to other eukaryotic taxa will also be discussed.

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Population Genetic Aspects of Spore-Killing in *Podospora anserina*.

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Experimental population genetic studies were made to understand the evolution of spore killing, a form of meiotic drive in the ascomycete fungus *Podospora anserina*. Spore killing is an easy to measure phenotype; Asci resulting from crosses between a spore killer strain and a sensitive (non spore killer) strain contain only two instead of the normal four ascospores, all of them having the spore killer genotype.

To understand the significance of spore killing in evolution a survey was made over several years of the natural population around Wageningen (The Netherlands). Among 73 new strains isolated from horse and rabbit dung, 17 strains contained some type of spore killing. At least 5 different types of spore killing could be identified. These results infer that spore killing is a common phenomenon and more types can co-evolve with sensitives in a so far stable situation.

Outcrossing or heterokaryon formation between isolates is a necessity for spread of selfish genetic elements within a population. However outcrossing is thought not to occur between different fungal individuals in nature. The secondary homothallic fungus *P.anserina* is capable of selfing and does not need outcrossing to reproduce (*P.anserina* produces only sexual offspring). We tested strains for outcrossing on natural media (horse dung) and found percentages ranging from 0 to 2%.

Also preliminary results are presented of competition experiments between different killer types or killer and sensitive isolates. In these experiments even higher percentages of outcrossing were found.

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ASPERGILLUS NIGER AND ITS VIRUSES

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In a world-wide survey of black *Aspergilli*, about 10 percent of the isolates appear to contain double stranded RNA fragments. These fragments form parts of different mycoviruses and the number and sizes of dsRNA bands detectable with agarose gel-electrophoresis differ greatly among the virus-containing strains.

Presence of virus is not restricted to a certain type within the *A. niger* group: Viruses can occur in strains with various types of mitochondria.

Virus free and infected strains were studied in several experiments. For this purpose infected strains were cured and virus free strains were infected, the latter either spontaneously (in the very few heterokaryon compatible combinations) or by protoplast fusion. Comparing these strains with their 'ancestor' showed that the mycoviruses can have a slight negative effect on mycelial growth rate and spore production. Only in one case the host debilitates strongly and forms perceptible non-sporulating sectors in its colonies. Thus reducing the colony growth rate by a 35 % instead of a mere 5% and the production of spores even by 70% in comparison to the same non-infected strain.

Effectively all asexual offspring is infected with virus. 'Horizontal' transfer however appears to be very limited. Strains are mostly vegetative incompatible with one another and we hypothesize that this barrier in the *A.niger* group is often strong enough to prevent the horizontal transfer of virus. To test this currently transfer experiments are carried out to study possibilities of transfer under more and less stringent conditions.

The generation of genetic diversity in asexual *Taraxacum officinale*.

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P1.

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The functional significance of sexual reproduction is still one of the important questions in evolutionary biology. The common dandelion (*Taraxacum officinale*) seems to be an almost ideal model organism to test the numerous hypotheses that have been suggested in the last 15 years. The common dandelion occurs in two forms: 1. sexual diploids ($2x=16$): outcrossing (self-incompatible) hermaphrodites and 2. asexual triploids ($3x=24$): autonomous, obligate apomicts, that produce pollen.

Allozyme studies have indicated that asexual populations consist of many clones. It has been suggested that new $3x$ clones are produced by crosses between $2x$ sexual mothers and $3x$ apomictic fathers in mixed sexual-asexual populations. Evidence comes from wide experimental crosses and shared allozymes and rDNA polymorphisms. However, part of the diploid offspring in wide crosses, appears to be due to selfing, as a consequence of the breakdown of the SI. system. Shared polymorphisms of nuclear inherited genes, could be due to introgression of genes of apomicts into the sexual gene pool and do not prove a local origin of new apomictic clones.

Until now, there are no data on the frequency of formation of new clones in natural mixed sexual-asexual populations. Therefore the breeding system of offspring from field pollinated sexual plants in mixed populations was studied. The results show that although arising at low frequencies, each year several thousands of new clones are produced in medium sized mixed populations. It is assumed that these new clones spread gradually into the asexual range.

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Delayed maturation in semelparous populations with non-equilibrium dynamics.

Evolutionary arguments explaining 'risk aversion' strategies incorporate 'environmental variability' in the appropriate fitness measures. Environmental variability can be a consequence of stochastic processes, but fluctuations in population size driven by non-equilibrium population dynamics, can also affect life history parameters through density-dependence.

For semelparous organisms with life cycles that are typically longer than one reproductive season, delayed maturation can be seen as an exchange process between temporal populations. In organisms with a strictly biennial strategy, individuals breeding in even and uneven years actually belong to different temporally separated populations. This has some consequences when modeling the evolutionary dynamics of delayed maturation in such populations.

We studied the evolutionary dynamics of delayed maturation in a semelparous two-phase model with density-dependent fertility and clonal reproduction. We considered all possible attractors of the resident population(s), basing our conclusions on invasion exponents calculated for invasions into any mixture of temporally separate populations, for parameter values where such a separation occurred.

This study shows that non-equilibrium dynamics selects for a nonzero probability to delay maturation. Coexistence of delaying and non-delaying strategists is possible though, in cases where the non-delaying strategy has a periodic attractor in the absence of the other type. If there is a nonzero delaying probability that is evolutionary attracting, then it is a continuously stable strategy.

Intuitively, we might expect that the evolutionary walk will halt at a bifurcation boundary, where the fluctuations in population size disappear. This is not the case. The evolutionary walk never reaches a bifurcation boundary of the population dynamics.

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Responses and correlated responses to artificial selection on leaf length in *Plantago lanceolata*, L.

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P. lanceolata, the Ribwort Plantain, occurs in a wide range of habitats and has a variable growth form. Clear differences in a number of morphological traits exist between populations. Plastic responses to light conditions result in a range of phenotypes similar to the range resulting from genetic differences between populations. The specific associations of morphological traits seem to be caused by variation in a common developmental process.

An artificial selection experiment was conducted in two contrasting light environments to answer the following questions:

- 1) Does artificial selection for one trait (leaf length) lead to correlated responses in other traits?
- 2) Can selection for one trait change the associations among traits?
- 3) Does artificial selection in one environment lead to correlated responses in the trait in the other environment?
- 4) How does selection influence plasticity in growth form in reaction to varying light conditions?

Large direct responses in leaf length were found after bidirectional selection. The correlated response in the other environment was in the same direction but smaller than the direct response. Selection for leaf length also resulted in correlated changes in other traits. However, in several cases selection affected the specific association among traits. Plasticity of some plant characters was also influenced by selection while in other traits plasticity remained unchanged. These results suggest that the associations of traits found in *P. lanceolata* are not due to developmental constraints, but are brought together by natural selection.

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Natural variation in flowering time in *Arabidopsis thaliana*.

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Genetic variation in flowering time was studied in four natural populations of *Arabidopsis thaliana* (Thale Cress), using greenhouse experiments. Two populations from ruderal, transient sites flowered early, two others from old river dykes late. However, the late flowering plants flowered almost as early after cold treatment (vernalization) of seeds. In the F_2 of crosses between early and late plants, a 1:3 ratio of early vs. late was found, indicating the presence of a dominant major gene for late flowering. In *Arabidopsis*, only one vernalization responsive gene is known that causes late flowering with lateness dominant: FRI. Linkage with microsatellite markers is currently studied to see whether the flowering time gene that segregates in the F_2 's indeed maps close to the FRI locus.

Mutagenesis in the lab has generated early flowering mutants at the FRI locus from late flowering wild types, but not the other way around. In nature, recessive early flowering ecotypes have been found in many different areas world wide. This suggests that late flowering could be the primitive state in *Arabidopsis*, from which early flowering has evolved on several occasions and in different habitat types (for instance at ruderal sites, but also in habitats with short growing seasons, or with severe winter cold).

The plants from ruderal sites presumably have a very flexible life cycle. They can be summer or winter annual, may have two distinct generations per year, or individual plants may have two reproductive periods in their life. The strong vernalization response of plants from the dykes makes their life cycle strictly winter annual. It appears that a single gene can dramatically change the life history of *Arabidopsis*.

**Host-plant species as a factor influencing genetic diversity
in populations of aphids *Aphis gossypii***

T3

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Part of the evolutionary biology of insect-host plant interactions can be assessed from knowing if and how genetic variability in conspecific populations is associated with different types of resources and how biological traits of the insects are acting on this variability (Futuyama & Peterson 1985). From that point of view, it seems interesting to study the correlation between the genetic diversity in aphid populations and the diversity of ecosystems in which they are encountered.

Among aphids, the species *Aphis gossypii* is cosmopolitan and extremely polyphagous. It is one of the most important pest of vegetable crops in greenhouses, tunnels and open fields (tomato, sweet pepper, cucumber, zucchini, melon, etc) in citrus orchards, in cotton fields or on flowers. This aphid is an effective vector of several plant pathogenic viruses and it is becoming more and more resistant to insecticides. Therefore, for pest management it could be important to be able to differentiate aphid genotypes on different host-plants in different environments.

Variability in biological features, such as fecundity or virus transmission, between distinct clones of *A. gossypii* is detectable but genetic markers discriminating such clones are hardly identified. This paper presents the level of variability in random amplified polymorphic DNA (RAPD) patterns obtained for *A. gossypii* individuals collected in fifteen populations from different locations and host-plants.

Isozyme variation in relation to ecotypic differentiation and population size in *Silene nutans*

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Silene nutans is a diploid, predominantly outcrossing, herbaceous long-lived perennial. It occurs in xeric habitats on calcareous and siliceous bedrocks (pH range from 3.8 to 8.0). In Belgium, at the North Western limit of its Eurosiberian distribution range, it is a rare species with disjunct and marginal populations. There, it has evolved two edaphic ecotypes, a silicolous (Si-) and a calcicolous (Ca-) one, partially genetically isolated, which show contrasting morphological traits and reproductive characteristics.

Genetic diversity and population genetic structure were examined in relation to ecotypic differentiation and population size for seven allozyme loci in 34 populations of *S. nutans* (16 Si- and 18 Ca-).

The results show that *S. nutans* maintains a considerable genetic variation at both ecotypic and population levels, which does not support the hypothesis of low genetic diversity for marginal and disjunct species. Genetic diversity values of both ecotypes are typical of herbaceous long-lived perennials and of xenogamous species.

Genetic distance measures, cluster analysis using UPGMA on the distance matrix and exact tests for population differentiation reveal that the populations are differentiated according to their ecotypic property and that this differentiation consists of discontinuous variation. Both ecotypes show the same level of genetic variation, similar population genetic structure and a low level of differentiation among populations. Estimates of gene flow calculated by Slatkin's (1993, *Evolution* 47: 264-279) and Wright's (1951, *Ann. Eugen.* 15: 323-354) methods suggest that an efficient gene flow is occurring between adjacent populations within each ecotype.

Finally, no correlation is found between population size and any measure of genetic variation. This can be explained by long-lived perennial habit of the species, by an outcrossing breeding system and by an intense interpopulation gene flow, that can promote the maintenance of a high genetic diversity in spite of the scattered distribution and the small size of the populations.

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Inference on ancient population genetic parameters from sequence data on multiallelic mating system loci in plants: a dream or a reality?

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Recently, analyses of sequence data from multiallelic sporophytic and gametophytic self-incompatibility loci in plants have given evidence for the occurrence of transpecific polymorphisms dating to more than ten million years. It has been shown that these observations are compatible with a model of balancing selection acting on these loci. The simultaneous development of molecular and theoretical investigations on this topic have opened up the perspective of inferring some population genetic parameters, such as population size and structure, gene flow, the occurrence of population bottlenecks, in ancient times. In this talk I will discuss the theoretical models and show how they can be used for inference purpose, with an emphasis on the bottleneck issue. Then I will present some analyses of sequence data based on single-locus population samples and point out the discrepancies with theoretical expectations and the limits of the approach. At present the models are not fully validated by the available data. A discussion on the causes of these discrepancies and on a possible future of plants paleo-genetics will be presented.

Genetic relationships among *A.alba* and the relic population of *A.nebrodensis* based on RAPD markers and chloroplast DNA variation.

T5

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A. nebrodensis is one of the most relevant examples of a relic species in Europe, with a very limited distribution and in an evident state of regression. Its actual natural range has been reduced to a single population located in a very restricted area on the Madonie mountains, in Sicily: only 29 trees are considered to belong to this species.

Little is known about the origin of this species and the phylogenetic relationships with other *Abies* species. Some authors have hypothesized that *A. nebrodensis* is originated from the southern populations of *A. alba* as a consequence of isolation during the post-glacial period; on the other hand there is also an contrasting hypothesis of an independent origin of these species.

The aim of this work was to use molecular markers for clarifying genetic relationships among the unique population of *A. nebrodensis* and some Italian *A. alba* populations.

RAPD markers were used in order to estimate genetic variation within and among populations. Out of 60 primers tested, 12 resulted in polymorphic banding patterns both within and among populations and showed a high reproducibility. The level of RAPD differentiation among *A. nebrodensis* and *A. alba* is much higher than those found among *Abies alba* populations located more than 1000 km apart: these results seem to confirm the hypothesis that the two groups of populations belong to different taxonomic groups.

Two chloroplast DNA spacer regions between two pairs of tRNA genes were amplified and restricted with different enzymes. The amplification products were then cloned and sequenced. No differences in the size and in the restriction patterns were observed among the studied populations. The sequences of the intergenic spacers are very useful for evolutionary studies of related species: the DNA sequence of *A. nebrodensis* was compared with the same sequence of other *Abies* species using an alignment programme. The results showed a low sequence divergence between the different species.

A COMPARISON OF GENETIC VARIABILITY BETWEEN MONO- AND POLYPHAGOUS CHRYSOMELID BEETLES OF THE GENUS *PHYLLOTRETA*: A CASE STUDY OF THE NICHE WIDTH-VARIATION HYPOTHESIS

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The niche-width variation hypothesis (Van Valen, 1965) postulates a positive relationship between niche-width and morphologic or genetic variability, niche-width being defined as the proportion of some multidimensional resource space used by a species in a community (Shugart, 1973). For several insects a positive correlation between niche-width and genetic variability has been demonstrated. In most studies niche-width was derived from geographic distribution or host plant use. We preferred to look at another evolutionary important niche component : host plant use. Phytophagous insects are dependant on a certain range of hostplants, which can be very narrow or very broad. Species probably have co-evolved together with their host plant(s), and are therefore an interesting group for studying the variation hypothesis. According to the niche-width variation hypothesis species living on a single hostplant should be genetically less variable than species with a large range of hostplants, even if the single hostplant is very abundant.

For testing this "modified" niche-width hypothesis we studied certain species of the genus *Phyllotreta*. Several species of this genus are mono- or oligophagous (*P. dilatata*, *P. tetragyna*), feeding on few closely related plants, while other species (*P. consobrina*, *P. cruciferae*, *P. nigripes*) are found on a variety of hostplants and are considered polyphagous. Allozyme electrophoresis was used to detect genetic variability. We studied several populations of each of these species and compared several measurements of genetic variability (polymorphism, heterozygosity per locus per individual [H] and gene diversity [He]). The results do not always support the "niche width-hypothesis" and are compared with those of other phytophagous insects (both specialists and generalists).

Shugart, H.H. & Blaylock, B.G. (1973) The niche-variation hypothesis : an experimental study with *Drosophila* populations. *The American Naturalist*. 107 : 575-579.

Van Valen, L. (1965) Morphological variation and the width of the ecological niche *The American Naturalist*. 99 : 377-389.

Melanic genes: their effects on fitness
Verhoog M, Brakefield P & Holloway GJ

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Melanic genes, their effect on fitness.

Industrial melanism continues to be a textbook example of the evolution of an adaptive trait by natural selection. The understanding of the phenomenon is still incomplete because theoretical studies indicate that the melanic alleles must have 'non-visual' effects on fitness in addition to visual effects, such as predation by birds which hunt moths by sight. Melanic stocks of the flour moth, Ephestia kuehniella, have been used to examine these non-visual components of fitness in a 'model' laboratory system. In this experiment the components of fitness have been measured for two melanic genes and six individual genotypes will be described.

Temporal patterns in the genetic structure of a parasitised population of a clonal freshwater bryozoan

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Empirical and theoretical studies suggest that: (i) parasites are ubiquitous in animal populations, and; (ii) genetic novelty, created by sexual reproduction, may promote resistance to common parasites. However, some animals present a paradox: they reproduce predominantly asexually, and show low levels of genetic variability, but still sustain high levels of parasitism. An example is the colonial freshwater bryozoan *Cristatella mucedo* which reproduces mainly asexually (clonally) and shows little intra- or inter-population genetic variability. Although many populations harbour myxozoan parasites, *C. mucedo* is common in isolated lakes and ponds throughout Britain.

We are using PCR derived RAPD markers to conduct a longitudinal study of the diversity, abundance and relatedness of clones within a single population. The study encompasses a period of high infection rates by myxozoans followed by host population decline and subsequent recovery. Ecological sampling indicated that the population crash suffered by bryozoans reflected a parasite-mediated reduction of host fitness.

NATURAL HYBRIDIZATION BETWEEN *ORCHIS LAXIFLORA* AND *O. PALUSTRIS*
(ORCHIDACEAE) IN ITALY.

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The loose flowered orchid, *Orchis laxiflora* and the bog orchid *O. palustris* are differentiated in their morphology, genetics and ecology. The former prevails on wet grassland up to 1000 m, whereas the latter is typical of marshes, often at sea level. In the last centuries, human activity (deforestation, land reclaiming, agriculture) has strongly affected the range and local distribution of these two species, favouring the spread of *O. laxiflora*, severely reducing suitable habitats for *O. palustris*, and creating opportunities of secondary contacts between them. Several hybrid zones between *O. laxiflora* and *O. palustris* were detected in Italy (Rossi *et al.*, 1994), among which the following were genetically analyzed: – Bassa del Bardello, a reclaimed land near Ravenna (Romagna); – retrodunal areas south of Viareggio (Tuscany); – Bagnaccio, the bottom of a drained lake with sulphureous water near Viterbo (Latium); – several marshes near Lecce (Apulia). Different genotypes (parental, F_1 and F_n hybrids, backcrosses, introgressants) were recognized on the basis of 17 loci found diagnostic between *O. laxiflora* and *O. palustris* over the 30 studied. The proportion of F_1 hybrids was found to decrease proceeding from north to south (Romagna: 25%; Tuscany: 16%; Latium: 15%; Apulia: 7%). A limited number of recombinant and introgressed classes (less than 10 %) was detected, indicating a low hybrid fertility. The lower hybridization rate observed in Southern Italy (Apulia) seems to be related to a partial ecological segregation between *O. laxiflora* and *O. palustris* in this area with the former often associated with *Plantago crassifolia* and the latter with *Schoenus nigricans*.

Selection against transposable element insertions is stronger in *Drosophila simulans* than in *Drosophila melanogaster*.

T12

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The insertion site numbers of the transposable elements (TEs) copia, mdg1, 412, and gypsy were determined in various natural populations of *Drosophila melanogaster* and *D. simulans* by *in situ* hybridization. In *D. melanogaster* all elements except gypsy had many copies scattered over the chromosomes. In *D. simulans* only the 412 element presented a high number of insertions. The value in *D. simulans* was lower than in *D. melanogaster* suggesting a difference in effective population size according to Aquadro *et al.* (1988). In an attempt to explain the difference in copy number in both species and to test theoretical hypothesis of TE containment in genome, we have determined the proportion of 412 insertions on the X chromosome (related to the autosomes) in diploid genomes, haploid genomes, and interpopulation hybrids. In both species, the values obtained were lower than the value of 0.20 expected for the hypothesis of no selection against insertional mutations. Moreover the proportion of insertions on the X chromosome was significantly lower in *D. simulans* than in *D. melanogaster* (0.087 for *D. simulans* against 0.137 for *D. melanogaster* in diploid genomes; 0.102 against 0.146 in haploid genomes; 0.098 against 0.149 in interpopulation hybrids). These results suggest that selection is the main force acting against the mutational effects of TE insertions, and is stronger in *D. simulans* than in *D. melanogaster*, independently of effective species size.

Aquadro *et al.* 1988 The *rosy* region of *Drosophila melanogaster* and *Drosophila simulans*. I. Contrasting levels of naturally occurring DNA restriction map variation and divergence. *Genetics* 119: 875-888.

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In the study of variation of *Castanea sativa*, Turkey represents an area of special interest due to its complex biogeography and also because the centre of origin of this species is thought to be located in the Ponto-Caucasian region. Chestnut range extends from the Eastern Black Sea coast to the Mediterranean coast, i.e. from Eurosiberian to Mediterranean phytogeographic area. Previous studies based on isozyme analysis carried out on *Castanea sativa* from Turkey showed high genetic divergence between the Western and Eastern populations. Such divergence was also confirmed by morphological and physiological data. Furthermore, populations from Northern Bithynia, a geographically intermediate area, showed the highest polymorphism level and intermediate genetic distance values (Villani et al., 1992, 1994). Two hypotheses were attempted to explain such results: i) populations from Northern Bithynia are the product of introgression in a secondary contact zone; ii) the same populations represent a source for all European chestnut.

The aim of the present study was to evaluate the degree of genetic and morphometric differentiation both at inter and intra population level in order to provide further data to test the hypotheses. Two series of data sets were used: winter buds from 34 population samples across the chestnut range in Turkey; fruits from open pollinated trees (half-sib families) belonging to populations representative of the three main population groups previously found. Genetic data were obtained from electrophoretic analysis of 12 gene enzyme systems. Morphometric data were based on 13 fruit traits. The results highlighted the following: i) presence of three genetic clusters was confirmed both in the adults as well as in the progenies, with the central populations (Northern Bithynia) being intermediate and displaying the highest level of polymorphism; differences in the contribution to the interpopulation genetic divergence was observed among the loci examined; ii) high degree of outcrossing rate was observed in all populations studied; unlike adult samples, deviations from HW equilibrium were detected in the progenies (excess of heterozygotes); iii) variation in morphometric traits was correlated to variation in allozyme frequencies and it was also finely tuned at the regional scale.

These results are in broad agreement with the hypothesis of an early geographic isolation of the Eastern and Western groups of populations followed by extensive introgressive hybridization in the Bithynian region. The genetic structure of populations in the hypothesized hybrid zone is presently investigated at the microgeographic scale. Possible pre- and postzygotic isolation mechanisms occurring between populations is also tested by controlled cross experiments.

Ecological versus evolutionary stability: does natural selection promote persistence of host-parasitoid interactions?

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IT 10.

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When attempting to explain phenomena and processes at the population level from the individual level, the primary question is whether properties of individuals make a difference to these processes. If so, the next question is which of these properties are favoured by natural selection. This approach emphasises the interplay between ecological and evolutionary processes: the direction of natural selection depends on the environment, and part of that environment (the number and properties of conspecifics) depend on the outcome of this selection process. We address these questions for a host-parasitoid interaction in a patchy environment.

The system we envisage is based on a host-parasitoid interaction well studied in both the field and the laboratory: parasitoids of the genus *Leptopilina* attacking larvae of *Drosophila* on Stinkhorns. Parasitoids, after landing on a patch (a Stinkhorn), search for some time for hosts (*Drosophila* larvae) before moving to a next patch. The decisions on which patch to land and how long to search for hosts are crucial, both in terms of individual reproductive success and the overall distribution of parasitism over patches. The latter determines to a large extent the dynamics of the interaction. We therefore focus on patch arrival and leaving decisions.

We discuss two patch leaving rules, one based on the marginal value rule and assuming global knowledge of patch quality, and one in which parasitoids only get information from patches visited by them. Furthermore, we look at one arrival rule, where parasitoids only land on a subset of high quality patches. In all these cases parasitoids use the same rule but can differ in a parameter within this rule.

Firstly, we examined ecological stability. A null model, where parasitoids leave from and arrive on patches at random, always resulted in an unstable interaction. For both the leaving rules that were considered, the dynamics of the interaction was strongly influenced by the value of the parameter: the interaction was either unstable, chaotic or stable. For the arrival rule most parameter values resulted in an unstable interaction. These results clearly demonstrate that individual behaviour has a strong influence on processes at the population level. Secondly, the evolutionary stable parameter value is calculated using a simple invasion model. For both leaving rules it seems that natural selection pushes the system from both the unstable and stable region towards the chaotic dynamics. This would imply that in our model natural selection leads to persisting host-parasitoid interactions in a patchy environment.

QUANTIFICATION OF SWIMMING BEHAVIOUR OF FISH WITH AN AUTOMATED VIDEOMONITORING SYSTEM

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Fish have evolved a great diversity of patterns of locomotion. Quantification of swimming behaviour has been hampered by problems in gathering reliable, multiparametric data.

With an automated, personal computer based video-processing, object-recognition, and object-tracing system (BehavioQuant[®]) aspects of spontaneous swimming behavior of two fish species (zebra fish, *Brachydanio rerio*, Cyprinidae; cichlid, *Aequidens rivulatus*, Cichlidae) were recorded (groups of up to ten, untagged individuals in standard laboratory tanks). The primary data provided by the monitoring system are the time-correlated and individually assigned coordinates in two-dimensional projection.

Secondary parameters describe position and velocity of movement in horizontal and vertical direction, intraindividual temporal covariation of velocity and direction, and interindividual interdependencies. The two fish species show basically different patterns of locomotion and corresponding differences in the secondary parameters.

394 REPEATED DNAs AND CHROMOSOME EVOLUTION IN THREE T13 *GERBILLUS* SPECIES

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C-banding and fluorescence *in situ* hybridization (FISH) on chromosomes, and Southern blotting were used to analyze the constitutive heterochromatin in three species of the genus *Gerbillus* (Rodentia). Two of them namely, *Gerbillus nigeriae* and *G. aureus* are characterized by a large amount of heterochromatin which attains 50 and 40% of the total chromosome length respectively. Their heterochromatin is C-band positive but may be R-band positive or negative. The centromeric heterochromatin of the third species, *G. nanus* is unremarkable.

Two tandemly repeated DNA sequences of *G. nigeriae* (GN1 and GN2) have been isolated and characterized. Both share a 36 base pairs (bp) repeated unit which comprizes a 20 bp motif, also found in Primate alphoid and other repeated DNAs. The localization of GN1 and GN2 sequences on metaphase chromosomes of the three *Gerbillus* species was studied by FISH. In *G. nigeriae* and *G. aureus*, whose chromosome polymorphism suggests an actively going chromosome evolution, both GN1 and GN2 sequences were observed at various chromosome sites : centromeric, telomeric and intercalary. At contrast, the karyotypically stable *G. nanus*, which seems to have more ancestral karyotype and morphology possesses only GN1 sequences, localized in the juxtacentromeric regions.

The possible relationships between the chromosomal distribution of constitutive heterochromatin, the nature of repeated DNA sequences and the mode of chromosome evolution are discussed.

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Ukraine

The population structure in whiting is shaped during the spawning period. At this time, specimens from distinct populations are aggregated at the spawning grounds. As a result, the particularities of the gene pool of future generations are determined here. During the pelagic period of life, eggs, larvae, and fry are distributed in the surface layers, initially according to the major current patterns of the Black Sea; this is superimposed by numerous local eddies which are effective over periods of months to years. Nevertheless, adult fish return to the same spawning grounds where their parent-generation spawned. Such a condition has been described for many fish species which, like whiting, have pelagic eggs and larvae, including black halibut, pollack, and cod.

In this connection, I must link population structure with the spatially divided spawning locations in *Merlangius merlangus euxinus*. In literature is presented the distribution of whiting eggs and larvae near the northern and eastern coasts of the Black Sea. Examining egg distribution, however, reveals more than one area where whiting spawn.

As spawning ground location south on Black Sea corresponds with the results of our Institute's ichthyoplankton research. This confirms the hypothesis that whiting spawn in this region.

Spatially separated spawning grounds and the circulation system in the Black Sea support the conclusion that several populations of whiting can be found in the Black Sea.

The whiting has no horizontal migrations. Adult fish move only vertically from low depths to shallow water and back. They also move to shallow water for spawning, because their eggs and larvae appear in the zone of near shore eddies. Such mode of life may be a factor influencing the population structure of Black Sea whiting.

Robertsonian fusions, heterochromatin and chiasma
distributions in the karyotype evolution of grasshoppers

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The karyotypes of grasshopper species of two subfamilies: Acrididae and Oedipodinae (Orthoptera, Acrididae), were studied. The chromosome morphology, heterochromatin localization, the formation of synaptonemal complex and frequency and distribution of chiasmata were analyzed. We revealed two trends in the evolution of grasshopper chromosomes. The first one is reduction of chiasma frequency. This trend is found in the both subfamilies. The reduction of chiasma frequency is accompanied by robertsonian fusions of chromosomes in Acridinae, but not in Oedipodinae. The second trend is the formation of chromosome regions with the restriction of recombination. The restriction of crossing over is due to the absence of chromosome pairing. The regions with reduced recombination are located distally in Oedipodinae and proximally in Acridinae. The opportunity of Robertsonian fusions is supposed to depend on the localization of chromosome regions with restriction of recombination.

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Developmental genetic variation in interspecific hybrids of flour beetle
Wade MJ & Johnson NA T 4

Using interspecific hybrids between two species of flour beetles, *Tribolium castaneum* and *T. freemani*, we have discovered significant variation within and among *T. castaneum* populations for genes affecting antennal and limb development. Heritable variation in the degree of developmental asymmetries was also observed. Studies at different temperatures, spanning the range of environments experienced by this species, indicate further that there is a large component of genotype-by-environment variation involved in development. Because these genes are segregating within *T. castaneum* but produce scorable developmental phenotypes only in interspecific hybrids, it is also clear that gene interaction (epistasis) and canalization characterize the development of limbs and antennae in this species.

SEX ALLOCATION OF THE TWO FORMS OF *MYRMICA RUGINODIS* (Hymenoptera, Formicidae)

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T8

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Eusociality is defined by overlapping generations, shared brood care and reproductive division of labour. In social insects some individuals (workers) give up their reproductive potential to help others (queens) to reproduce more effectively. Workers can, however, gain fitness benefits through the reproduction of relatives. This concept of inclusive fitness states that helping behaviour is beneficial if its benefit/cost ratio exceeds the inverse of the relatedness between the two individuals. In eusocial Hymenoptera the evolution of eusociality is easy to understand because due to the haplodiploid sex determination system workers are more related to their sisters than to their own offspring. However, haplodiploidy also causes conflicts, because it leads to asymmetrical relatedness among colony members: If all the colony members are descendants of one reproductive pair the workers are three times more related to their sisters than to their brothers. Thus workers should prefer a female-biased sex ratio at the population level, but equal investment in both sexes is the queen optimum. However, ant colonies may have many queens per colony or the queen may mate multiple times. The effect of having multiple queens depends on the relatedness among them, whereas multiple matings by a queen always reduces conflict. Interestingly, individual ant colonies tend to specialize in producing unisexual brood. Three mechanisms have been proposed to explain this: i) colonies differ in the amount of total resources available to them ii) sexes differ in their dispersal ability leading to competition between related individuals iii) colonies differ in their relatedness asymmetry, that is, workers' relatedness to sisters compared to brothers.

We studied the sex allocation of the red ant *Myrmica ruginodis*, which has two social types. Macrogyne colonies tend to have one queen only and the queens are larger, whereas microgyne queens are smaller and colonies are multiple-queened. We excavated a total of 35 whole colonies (17 macrogyne and 18 microgyne) and measured queen number, colony size, number of male and female pupae and relatedness among colony members (as estimated from allozyme analysis of four polymorphic loci). Our results indicate that workers control the sex allocation of individual colonies of *Myrmica ruginodis* in response to the relative relatedness asymmetry of their colony. In the microgyne form also the competition for resources between related females affects sex allocation, pushing it towards more male bias.

Radiation and classification of the blowfly genus *Lucilia* (Diptera: Calliphoridae).

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The genus *Lucilia* (Diptera: Calliphoridae) is a small, relatively homogeneous group of metallic, green-blue, calliphorid flies commonly known as greenbottles. All species of the genus are morphologically similar and many species can only be reliably distinguished by the shape of the male genitalia.

The larvae of most species of the genus are saprophages, living in animal carcasses and proteinaceous waste materials. However, a small number of species have also evolved a specialised facultative ectoparasitic lifestyle, causing cutaneous myiasis, largely affecting sheep, although they may also strike a range of other wild and domestic animals and humans.

The *Lucilia* appear to have been originally and predominantly palaearctic in distribution. However, in addition to natural patterns of global radiation, in recent history as humans and domestic livestock began to move worldwide with increasing facility, a number of species appear to have been carried to new habitats, where they began to diverge genetically. In some cases, for species of veterinary importance, a relatively precise chronology can be constructed for these introductions. By the early 20th century *Lucilia* had been recorded in North and South America, South Africa, Australia and other regions of the Pacific.

Given its apparently recent radiation, the genus *Lucilia* is of considerable interest for studies of evolution and speciation, although, at present, the classification of the genus remains unclear. Discrete strains of some species are recognised while the integrity of other species is uncertain; some authors recognise sub-genera while others do not. In this paper we will first describe the current state of knowledge of the classification of the genus. We will then present a cladistic parsimony analysis designed to investigate phylogenetic relationships among *Lucilia* species, using presence or absence data based on morphological characters, as a first step towards elucidating the evolutionary relationships within the genus.

Non-orthologous evolution of alpha satellite DNA at the centromeres of humans and the great apes: analysis of a chromosome-specific chimpanzee alpha satellite repeat unit.

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Alpha satellite DNA is a tandemly repeated DNA family found at the centromeres of the chromosomes of primate species ranging from old and new world monkeys to higher primates and humans. The fundamental repeat unit of alpha satellite DNA is based on tandem diverged 169-172 bp monomers, which are often found to be organized in chromosome-specific higher-order repeat units. These sequences are subject to concerted evolution which results in a high degree of species-specificity and, within a species, chromosome-specificity.

The sizes and banding structure of chromosomes of man (*Homo sapiens* (HSA)), chimpanzee (*Pan troglodytes* (PTR) and *Pan paniscus* (PPA)) and gorilla (*Gorilla gorilla*) share a remarkable similarity, and the sequences are highly syntenic. It is of interest to ask if alpha satellite arrays at centromeres of homologous chromosomes between the different species are closely related (evolving in an orthologous manner), or if the evolutionary processes that homogenize and spread these arrays within and between chromosomes result in non-orthologous evolution of arrays.

In this study, we attempt to gain further insight into this dynamic evolutionary process between the alpha satellite arrays found on the chromosomes of humans and chimpanzees. By using PCR primers specific for the human chromosome 17-specific alpha satellite subset, we have amplified, cloned and characterized a chromosome specific alpha satellite DNA subset from the chimpanzee PTR genome. Hybridization on both Southern blots and in situ as well as sequence analysis shows that this subset is most closely related in human to chromosome 17. However, in situ chromosome analysis reveals that this subset is not found on the corresponding homologous chromosome in chimpanzee (PTR 19), but instead is found on PTR 12, which is homologous to HSA 2p. This study adds analysis of a chimpanzee derived chromosome-specific alpha satellite subset to the accumulating evidence that centromeric alpha satellite DNA undergoes dynamic evolutionary processes resulting in divergence of centromeric sequences despite the high degree of chromosomal similarity between the great apes and humans.

Studies of macroalgae biodiversity at the infraspecific level is rudimentary in comparison to higher plants. Especially, analysis of genetic diversity at the population level in relation with gene flow and breeding system have been particularly neglected. Marine environment is often considered as stable and characterised by high dispersal abilities. Therefore, magnitude of gene flow is supposed to be high and in particular within population spatial structuration is supposed to be non significant. Since few years, many studies tend to invalidate this fact but data mostly regard animal species and data about algae are still scarce. Moreover, algae are unique in having a wide variety of life cycles that involve haploid, diploid and haplo-diploid ones. These life cycles may strongly affect breeding system in different manners. Because haploid selection purges the genome of deleterious mutations at expressed loci, we might expect inbreeding depression to be minimal in species characterised by a prolonged haploid phase, and then selfing is expected to evolve in such species.

Influence of life cycle on breeding system and spatial genetic structure within a population were experimentally studied on an haplo-diploid red seaweed species: *Gracilaria verrucosa*. The life cycle is haplo-diploid with haploid female and male gametophytes, and diploid tetrasporophytes as free living individuals occurring together in natural populations. Haploid and diploid individuals are morphologically indistinguishable except when fertile (consequently we expect the same genes to be expressed in both phases). One population corresponding to a rock pool of about 100 m² was mapped and sampled (100 individuals), ploidy level and sex were determined for each individual.

Genotyping at a hypervariable single-locus DNA markers, a (TC)_n PCR-analysed microsatellite was done. Microsatellites are tandem repeat of short motifs (1 to 5 nucleotides, here a TC motif) highly polymorphic through the variation of repeat number; leading to alleles of corresponding size. The most prone mutation process for microsatellites loci correspond to a stepwise mutation model. This implies that alleles of close sizes are more likely to be related than alleles with larger size differences.

The studied locus is presumably characterised by a very high mutation rate because it was highly polymorphic with 39 alleles revealed for 189 haploid genomes studied.

Breeding system was firstly estimated using heterozygote deficit measurement. The results suggest that the species is highly endogamous. However, this classical population genetics parameter could only be applied to diploid data. So an other method was developed integrating haploid data and based on spatial genetic analysis. The 3 following characteristics (1) occurrence of restricted gene flow (2) very high mutation rate of the locus and (3) step wise mutation model suggest that we may expect positive correlation of allele sizes over short distances within a population. To test this hypothesis, spatial autocorrelation of allele sizes was calculated within the population. Significant positive correlations of allele sizes did occur over short distances (below 1 metre). These data suggest that inbreeding does occur and that a genetic micro differentiation in space may occur within a population. Moreover, these results are the first experimental data that tend to confirm the step by step mutation process of microsatellite sequences.

Population genetic structure of a haplo-diploid red seaweed *Gracilaria verrucosa*: within population spatial genetic structure, red algae.

Key words: life cycle, haplo-diploidy, *Gracilaria verrucosa*, microsatellite, breeding system, within population spatial genetic structure, red algae.

differentiation and breeding system

Microevolutionary processes in *Daphnia* due to predators

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Abstract

Daphnia spp. (Crustacea: Cladocera) respond specifically to different types and intensities of predation reacting on kairomones which are emitted by the predator. Two effects of the predator are distinguished: 1. indirect effect (kairomone), acting on an individual basis; 2. direct effect (size-selective predation), shaping the population composition. Both effects are met by the daphnids by adjusting the life-history to the predatory regime in order to maximise fitness. To gain more insight in the intra- and interpopulation differences in heritability and fitness is the aim of this study. To achieve this, the response of one *Daphnia* species (*D. galeata*) to two different predatory regimes (*Chaoborus flavicans* (phantom midge), preferring small prey items; *Gasterosteus aculeatus* (stickleback), preferring larger prey items) is tested in laboratory experiments on individual and population level. From two historically different locations, one of which without *Gasterosteus* predation and one without *Chaoborus* predation, a number of clones are sampled and tested in laboratory experiments. Initially the influence of predator specific kairomones on life history traits and phenotypic plasticity of individual daphnids are investigated in a multifunctional set-up. This includes exposure to only one single kairomone as well as to a mixture of *Chaoborus* and *Gasterosteus* kairomones. The next step are experiments on population level to transfer the value of clonal specific adaptation and plasticity into fitness in the field. This will be done by exposing aquarium populations to kairomone conditions as in the previous experiment and monitor changes in population composition. The same experimental set-up, replacing the kairomones by living predators, will also be used to test to what extent the adjustments made to specific predatory regimes are translated to and incorporated in the genetic code of an individual to benefit future generations. The results will be compared to the outcome of an individual-based model (OSIRIS).

MHC-dependent mate preferences in humans

T1

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One substantial benefit of sexual reproduction could be that it allows animals (or humans) to rapidly react to a continuously changing environmental selection pressure such as coevolving parasites. This counteraction would be most efficient if the females were able to provide their progeny with certain allele combinations on loci which may be crucial in the parasite-host arms race, e.g. the MHC (major histocompatibility complex). Here, we show that the MHC influences both body odours and body odour preferences in humans, and that the women's preferences depend on their hormonal status. Female and male students were typed for their HLA-A, -B and -DR. The men wore a T-shirt during two nights. On the following day, the women were asked to rate the odours of six T-shirts each. They scored male body odours as more pleasant when they differed from the men in their MHC than when they were more similar. This difference in odour assessment was reversed when the judging women were taking oral contraceptives. Furthermore, the odours of MHC-dissimilar men remind the test women more often of their own actual or former mates than do the odours of MHC-similar men. This suggests that the MHC influence human mate choice today.

the cost of sex for a hermaphrodite: how much does the flatworm *Dugesia polychroa* (Turbellaria, Platyhelminthes) pay?

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In species with two sexes the 'cost of sex' is the cost of producing males, which gives a hermaphrodite a twofold advantage in the case of a 1:1 sex ratio. This twofold advantage does not necessarily apply to a simultaneous hermaphrodite that reproduces asexually (produces parthenogenetic eggs or seeds), because it still has the cost of male allocation. Although it can increase its reproductive success up to twofold by reducing male investment, this requires additional anatomical and behavioural changes after transition to parthenogenesis, which is not the case in species with separate sexes.

The flatworm *Dugesia polychroa* is a simultaneous hermaphrodite that occurs in two biotypes: diploid sexuals and triploid pseudogamous parthenogens. We found that parthenogens have fewer testes, produce less sperm and lay more cocoons than sexuals, indicating that they have gained a reproductive advantage over the sexuals. Surprisingly, we found no behavioural differences (mating frequency and duration) between both biotypes.

But there is also a benefit to the maintenance of the male function in parthenogens if they are still able to mate with sexuals. This can result in the spread of genes for parthenogenesis in a sexual population. In *D. polychroa*, triploid parthenogens produce haploid sperm which can fertilize the haploid eggs of sexuals in hybrid crosses. Using animals from a mixed diploid-triploid population, we investigated the conditions for gene flow from the triploid to the diploid subpopulation. Sexual and parthenogenetic worms copulated readily with each other even when given a choice. From sexual cocoons sired by a triploid father fewer young hatched, but these young grew at a similar rate as offspring of a sexual father, some reaching adult size within four weeks. Thus, conditions for gene flow from parthenogens to sexuals are met. It was previously known that new triploid parthenogenetic lineages can arise in the F2 generation after a hybridisation event between both biotypes. We found 3 triploid young among a sample of 229 offspring from diploid mothers. Although this is not a considerable cost of sex it may be an important source of genetic variation in the parthenogenetic population.

The above mentioned advantages may be balanced by specific disadvantages of parthenogenetic reproduction. Theory predicts that asexuals are more susceptible to parasites (Red Queen) and/or accumulate more deleterious mutations than sexuals. This may explain why the parthenogens produced a high proportion (about 30%) of infertile cocoons. An experimental design is proposed that uses the unique features of reproduction in *Dugesia* to estimate mutation loads of parthenogenetic lineages.

Plant Defense as a System of Cascading Reaction Norms. ARTHUR E. WEIS, *Department of Ecology and Evolutionary Biology, University of California, Irvine, CA, USA 92717*. AND D. GORDON BROWN, *Department of Biology, St. John's University, Collegeville, MN, USA 55108*.

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Phenotypic plasticity can be shaped by selection when development occurs in environments that vary over space or time. An important component of environmental variation for plants is the abundance of their natural enemies. One would predict a general decline in plant fitness as herbivore density increases. Thus plant performance can be depicted as a norm of reaction in response to herbivore abundance. The shape and slope of this declining function will be influenced by the two general components of plant defense—resistance and tolerance. Resistance mechanisms alter the attractiveness or palatability of the plant and thereby influence the amount of tissue damaged by herbivores. Tolerance mechanisms influence the plant's ability to regrow after damage is inflicted. Resistance and tolerance can themselves be depicted as norms of reaction. The expected damage level, as a function of herbivore density, is the resistance reaction norm. Tolerance reaction norms show fitness as a function of damage received. When the two reaction norms (damage $v.$ herbivore density, and, fitness $v.$ damage) are combined, damage terms cancel to make fitness a function of herbivore density.

In effect, the resistance-tolerance dichotomy in plant defense is analogous to the habitat preference-performance dichotomy in animals. The effectiveness of a resistance allele determines if the plant develops in a high or low damage environment. The selective advantage of that allele, however, will depend on the plant's ability to tolerate damage. Similarly, the selective advantage of alleles affecting regrowth potential will depend on the likelihood of plant damage. Thus resistance and tolerance have epigenetic effects on fitness.

Our current long-term field experiments use the reaction norm approach to evaluate the variation in selection intensity on defense components induced by the wax and wane of herbivore population density. We are using goldenrod (*Solidago altissima*) and defoliating beetles (*Trirhabda* spp.) to measure genotypic variance in resistance and tolerance reaction norms for 35 cloned plant genotypes drawn from a natural population. In one experiment where we manipulated beetle densities, the increase in % defoliation with increase in beetle release densities appears as a saturating curve. Both the plant genotype and the genotype \times release density interaction effects were highly significant in an ANOVA. In another experiment with the same 35 genotypes, several growth performance and fitness components declined linearly with % defoliation. Although the genotype effect was highly significant, the genotype \times defoliation level term was not; this indicates genetic variance for overall growth performance, but not for tolerance. Correlations between parameters of the resistance and tolerance reaction norms suggests that plant genotypes with the greatest potential growth vigor are the most heavily attacked. The heavy attack on the potentially most vigorous genotypes reduces their realized performance to levels similar to plants of lower potential. Thus, differential herbivory on goldenrod genotypes reduces genotypic variance in fitness at high insect density.

THE *PIERIS NAPI*/*BRYONIAE* HYBRID ZONE AT PONT DE NANT, SWITZERLAND:

NO SELECTIVE IMPORTANCE OF THE TWO HOST PLANTS

ALLIARIA PETIOLATA AND *BISCUTELLA LAEVIGATA*

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Pieris napi and *Pieris bryoniae* are widespread in Switzerland but occupy different habitats. *Pieris napi* is found at elevations below 1200 m whereas the taxon *Pieris bryoniae* is most common in alpine habitats. At Pont de Nant in the Swiss Alps both taxa hybridize in a narrow zone at approximately 1200 m, the boundary of the *napi/bryoniae* hybrid zone corresponding to the ranges of host plants. The preferred cruciferous host plant in the *bryoniae* habitats is *Biscutella laevigata* (Lorkovic, 1962; Petersen, 1963). This food plant is absent in the *napi* habitat and the *napi* larvae seem to live oligophagous on several other cruciferous plants (Lorkovic, 1962; Petersen, 1963) the most common of which at low elevations is *Alliaria petiolata*. Varga (1967) proposed that this discontinuity in the distribution of host plants could have lead to adaptation of the two taxa to different food plants and by this way to partial reproductive isolation as it is the case in the *Papilio glaucus/canadensis* hybrid zone in North America where adaptation to host plants comprise an important selection pressure (Scriber, 1982; Lindroth et al., 1988b) probably contributing substantially to the hybrid zone dynamics.

Therefore, in this study the hypothesis was tested in how far the two taxa and their F1-hybrids are adapted to their sympatric hosts *Alliaria petiolata* and *Biscutella laevigata*, respectively, and whether adaptation to hosts is an important factor maintaining the hybrid zone. Adaptation to host plant measured in terms of duration of larval developmental time and larval mortality rate doesn't seem to produce any selection differential: neither for developmental time nor for mortality rate a significant interaction between crosses and host plant was found indicating larvae of all crosses grew equally well on both food plants. Larval developmental time was most strongly affected by temperature conditions ($P < 0.0001$) and photoperiod ($P < 0.0001$). In addition, there was a strong interaction temperature x photoperiod ($P < 0.0001$) with short photoperiods being especially effective in prolonging developmental time at low temperatures. Mortality rate only differed significantly in dependence of temperature ($P < 0.0001$) with mortality rates being increased by a factor of 1.5 at low temperature.

Interactions between systemic diseases and plants in natural plant populations

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Many systemic and perennial smuts and rusts occur in high frequencies in natural plant populations. One such example is the rust *Puccinia minusensis* which frequently infect more than 50% of individuals in populations of the clonal plant *Lactuca sibirica*. A range of field and greenhouse studies were set up to study this interactions. The results show that to understand this and similar interactions between systemic diseases and their host plants we need a much more open and wider view on how these interactions work than is given from the more standard "susceptibility-resistance-host density" explanations that are used. It is concluded that we need: 1) Long-term studies. 2) Studies on different systems. 3) To understand the importance of e.g. life-history strategies of both host and pathogen. 4) Information about how abiotic and biotic factors affect the interaction.

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Wolbachia are cytoplasmically inherited bacteria found in reproductive tissues of many arthropod species. These bacteria are associated with reproductive alterations in their hosts, including parthenogenesis, reproductive incompatibility and feminization. A survey of neotropical and neotemperate insects shows that 10-15% of species have Wolbachia, encompassing all the major orders. A fine-scale phylogenetic analysis was undertaken using DNA sequences from *ftsZ*, a rapidly evolving bacterial cell-cycle gene. *ftsZ* sequences were determined for 39 different Wolbachia strains from 32 different species of insects and one isopod. The following results were found, (a) there are two major divisions of Wolbachia (A and B) which diverged 58-67 MYA based upon synonymous substitution rates, (b) a general concordance is found between the *ftsZ* and 16S rDNA phylogenies, indicating that these represent bacterial strain rather than simply gene phylogenies; however, a possible example of recombination between A and B division bacteria may have occurred in the feminizing Wolbachia present in an isopod, (c) extensive horizontal transmission of Wolbachia has occurred between insect taxa, including different insect orders; one strain in particular (designated Adm) shows extensive recent horizontal transmission, (d) there is an association between the Wolbachia found in a parasitic wasp (Nasonia) and its fly host (Protocalliphora), suggesting exchange of bacteria between these species, (e) parthenogenesis induction has evolved multiple times among the Wolbachia, and (f) some insects harbor infections with more than one Wolbachia strain, even within individual insects.

Single and Double infections were further studied in the parasitic wasp Nasonia vitripennis. Wild-type strains of this wasp typically harbor infections of both A and B bacteria. However, prolonged diapause (the larval overwintering stage of the wasp) can result in stochastic loss of one or both strains of bacteria, giving sublines from a single lineage that contain A+B, A only, B only or no bacteria. Crosses between A and B sublines shown nearly complete reproductive incompatibility between them. Thus, Wolbachia can be responsible for the rapid development of bidirectional reproductive incompatibility, even within a single strain. Evolutionary implications of these findings are discussed.

SIMULTANEOUS OPTIMISATION OF SEX ALLOCATION AND CLUTCH SIZE

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Given a fixed amount of resource to expend on reproduction a sexually reproducing organism must decide how many offspring to produce (defined as the clutch size) and how to allocate resources between the two sexes (defined as sex allocation). Normally, clutch size and sex allocation considerations can be isolated, but if females produce single sex broods then the optimal sex allocation strategy depends upon the clutch size of broods and vice versa.

In this talk I shall consider the optimal reproductive strategy of a female parasitoid who lays predominantly single sex broods. I will first present a model which predicts that the optimal clutch size and sex allocation strategy of a female should depend upon the extent to which she is host and/or egg- limited. A host-limited female is expected to die before she has deposited all of her eggs, while an egg-limited female is expected to run out of eggs before she dies. Then, I will go on to report field data from seven parasitoid species in the genus *Achrysocharoides* Girault and field experiments with one of those species (*A. zwoelferi* Delucchi) which provide support for the model described above.

***Aucoumea klaineana*: A Pleistocene success story now in decline ?**

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Changes in vegetation over the last 10,000 years in the Lopé Reserve, central Gabon, resulting principally from movements of the forest-savanna boundary, have been reconstructed by a combination of mapping of modern vegetation patterns, pollen profiles and dating changes in $\delta^{13}\text{C}$ values in soil organic matter. Savannas have existed within the rain forest throughout this period, but their extent has varied from several hundred to many thousands of km². These changes have resulted, in part, from changes in climatic conditions, but human demographic changes have also played a vital role. The earliest known human remains in the area are estimated to be 350,000 years old. Through their use of fire these peoples may have had a profound effect on vegetation dynamics, particularly during times of climatic stress.

In the absence of fire three species of large forest tree, *Aucoumea klaineana* (Burseraceae), *Lophira alata* (Ochnaceae) and *Sacoglottis gabonensis* (Humiriaceae) are able to establish successfully in savanna. A vegetation succession follows which has resulted in the formation of large stands of forest in which one or more of these species dominate. However, their seeds seem unable to establish under a closed canopy and all three species become rare or absent in later successional stages.

Aucoumea klaineana is an endemic species whose distribution is restricted to the southern two thirds of Gabon. We suggest that it is a species which adopted a highly successful reproductive strategy during a period of forest expansion, but because of its dependence on a dynamic forest-savanna interface it is now in decline in mature forest. It is, in effect, a victim of its own success. Other endemic species, both plant and animal, are also abundant close to the forest savanna interface in Lopé, emphasising the importance this habitat may have in the evolution of the African rain forest system.

Gene Families, Partial Functional Redundancy and Genetic Stability by Adam S. Wilkins, BioEssays, Company of Biologists, Ltd., 140 Cowley Rd., Cambridge CB4 4DL, U.K.

The genetic basis of developmental stability, "canalization", was one of the chief concerns during the 1940s and '50s of C.H. Waddington, the great developmental geneticist who worked at the University of Edinburgh. Today, several kinds of specific genetic mechanism can be envisaged to explain canalization. In this talk, the focus will be on evidence that one major element in developmental stability is partial genetic functional redundancy, involving paralogous genes. Recent examples involving neurogenesis in Drosophila and limb development in the mouse will be reviewed. Yet, while partial functional redundancy of paralogues can provide developmental stability and, hence, have selective value as a stabilizing force, much circumstantial evidence suggests that initial selection for paralogues is for new developmental functions, made possible through differential regulation of the gene duplicates. Some of these findings will be summarized. Partial genetic functional redundancy can act, therefore, either as an innovative or conservative force, depending upon the evolutionary stage. The talk will conclude with a discussion of the need to resume Waddington's research programme, with an analysis of the molecular basis of "background genotype" effects on expressivity and penetrance of genetic morphological defects, in light of contemporary concepts and employing the armoury of modern molecular tools.

How to analyse the genetics of phenotypic plasticity?

Jack J. Windig

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The genetic background of phenotypic plasticity has been analysed in many different ways. The aim of this research was to compare the different ways and identify their power and possible bias. The different ways of analysing plasticity fall into two categories: genetic correlations across environments and heritability of plasticity. For both categories many variations exist. The different measurements are however related and from one measurement another can often be calculated. Large datasets with a balanced half-sib family structure and a split family design were generated from linear reaction norms. In Monte Carlo simulations the power and bias of all the different methods were compared for two environments. Additive genetic correlations of -1, 0 and 1 with equal additive variances and unequal additive variances in both environments were analysed. Not all the methods were equally reliable, but most were in good agreement with expectations. Published work on the plasticity in wing pattern of a seasonally polyphenic, tropical butterfly is compared with the theoretical relationships derived above.

The body mass allometries as evolutionarily determined by the foraging process of mobile organisms

Lars Witting

Dept. Ecology & Genetics, University of Aarhus, Denmark

The evolution of the well known $\pm 1/4$ and $\pm 3/4$ exponents of the empirically established body mass allometries have remained an unsolved problem in evolutionary ecology. I show that these, and other, exponents of eight body mass allometries can evolve from the constraints associated to the foraging process of mobile organisms. More explicitly, it is the constraints by which the foraging process is regulated by intra-population interference competition and the constraints by which the exploitation of the individuals inhibit their own foraging that explain the evolution of the body mass exponents. The explained exponents include those of metabolic rate, life-span, population density, home-range, population energy use, maximum life-time reproduction, maximum rate of population increase, and the level of social behavior. The model suggests that some of the body mass exponents vary with the dimensionality of the foraging behavior, *i.e.*, they take the values $\pm 1/2$ when foraging occurs in one dimension, $\pm 1/4$ and $\pm 3/4$ when foraging occurs in two dimensions, and $\pm 1/6$ and $\pm 5/6$ when foraging occurs in three dimensions. In comparison the empirically established exponents of terrestrial organisms resemble the theoretical exponents for foraging in two dimensions, whereas the empirical exponents of pelagic organisms resemble the theoretical exponents for foraging in three dimensions.

Population dynamics by density dependent life-history evolution

Lars Witting

Dept. Ecology & Genetics, University of Aarhus, Denmark

Beginning with Malthus the classic theory of population dynamics is based on the assumption of no evolutionary changes in the growth rates of populations. This principle implies the population dynamics that is described by the Malthusian law, the logistic equation, and the Lotka-Volterra predator prey equations. Here I propose an extension of this theory by incorporating the evolutionary changes in the growth rates as they arise from density dependent selection through intra-population interference competition. The extended theory merges into the classic theory when heritable variation is absent. It is shown that the proposed theory explains the periods in the population cycles of forrest insects, and the cyclic changes in the phenotypes of small rodents. Amongst others, these include a peridic cycle in body mass, and the theory predicts that there exists also a periodic cycle in the sex ratio. The stability of the population cycle is influenced by the level of heritable variation, and if this level exceeds a certain threshold value the amplitude of the cycle will continue to increase and the population is expected to become extinct.

Selfish genetic elements as the optimal genetic code, and related talk on sex ratios and social communities

Lars Witting

Dept. Ecology & Genetics, University of Aarhus, Denmark

It is often believed that the evolutionary interest of cytoplasmic sex ratio distorters is in conflict with the interest of the individual, and that the sex ratio distorters are maintained in natural population because of their selfish component that generates a female biased sex ratio. To me this reasoning is up side down, at least within mobile organisms. Instead, I explain the evolution of a female biased sex ratio through selection by intra-population interference competition when combined with a relatively low population density. This evolutionary determinants of the sex ratio occurs independently of the underlying genetic system, and one optimal genetic code for a female biased sex ratio is a cytoplasmic sex ratio distorter. This approach explains also the widespread occurrence of female biased sex ratios and parthenogenesis in insects and poikilotherm vertebrates, against male biased sex ratios and the absence of pathogenesis in mammals and birds. Finally, it gives a solution to the problem that social communities with thousands of non-replicating workers per replicating queen have evolved in insects and not in vertebrates.

THE SHAPES OF APHID GALLS: INSECT CONTROL AND/OR PLANT CONSTRAINTS. David WOOL, Department of Zoology, Tel Aviv University, Tel Aviv 69978, ISRAEL.

The shapes of aphid-induced galls take various forms: leaf folds, small protuberances, marble-sized spheres, to very large bag-like structures or coral-shaped branching tubes. The shapes are aphid-specific and galls induced by different species - having distinct shapes - may occur on the same leaf. The galls are sometimes used as characters in taxonomic and phylogenetic studies of aphids.

However, aphid galls from the Middle East, Europe, North America and the Far East show surprising similarity when they are formed on the same plant part. Thus, for example, galls are formed on leaf margins or on axillary buds - by species in different aphid families - on different host trees and different continents - are often quite similar in shape. This raises the possibility that plant architecture, vascular structure, hormonal and nutrient transport efficiency and other plant characteristics restrict the type of galls that can be formed at each site. Moreover, insect interspecific and insect-hostplant interactions which may have determined the galling site of each species during its evolution, have thus determined the shape of its galls.

MtDNA Evolution of Neotropical Pitvipers (*Bothrops atrox* Species Group)W. Wüster¹, M.G. Salomão^{1,2} and BBBSP³¹School of Biological Sciences, University of Wales, Bangor, Gwynedd LL57 2UW, Wales, UK²Laboratório de Herpetologia, Instituto Butantan, Av. Vital Brasil 1500, 05503-900 São Paulo SP, Brazil³Butantan-British *Bothrops* Systematics Project (M.F.D. Furtado, S.A. Hoge, G. Puerto, M.G. Salomão, R.D.G. Theakston, R.S. Thorpe, D.A. Warrell & W. Wüster)

The *Bothrops atrox* species group comprises a complex group of highly variable pitvipers with a long history of systematic confusion. We use comparative sequencing of a section of the cytochrome-*b* gene (mitochondrial DNA) to infer the phylogeography and systematics of this group. Phylogenetic analysis of sequences of the *Bothrops atrox* complex and other species of *Bothrops*, using a variety of algorithms (Fitch-Margoliash, maximum likelihood, parsimony analysis) strongly supports the monophyly of the *Bothrops atrox* group. Phylogenetic relationships within the *Bothrops atrox* group are complex. Relatively low levels of among-population sequence divergence (<5%) suggest a radiation within the last 2 million years. Several of the nominal species currently recognised within this group do not represent historical entities. The results of this study are discussed with reference to observed patterns of variation in the morphology of these snakes, and with reference to biogeographical hypotheses for the Neotropical region, particularly the Pleistocene refuge hypothesis.

Genetic structuration on a microgeographic scale:
implications for the fixation of chromosomal mutants in
Sorex araneus (Mammalia, Insectivora)

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P13

Andreas Wyttenbach & Laurence Favre

The spectacular chromosomal evolution in *S. araneus* lead to the existence of about 30 chromosomal races. Therefore *S. araneus* has become a model species to study the link between genetic and karyotypic evolution and the formation of new races. Robertsonian fusions between acrocentric chromosomes (ancestral type) lead to metacentric chromosomes which subsequently spread through populations and became fixed. The mechanism by which the chromosomal mutants (metacentrics) were fixed is unclear.

The chance of establishment of a chromosomal rearrangement depends on its fitness and the population structure. Since it has been shown that fitness effects for *S. araneus* are of minor importance (Garagna et al. 1989, Wallace & Searle 1990) I shall focus on population structure. Simulation studies and population genetic models show that geographic subdivision of populations and migration rates strongly affect fixation probability. Similarly, stochastic processes can have a strong effect on the spreading and fixation of a new chromosomal rearrangement. On a population level no polymorphic markers are available for *S. araneus* and therefore its population structure remained mostly speculative.

The development of polymorphic microsatellite markers for 10 loci allowed an analysis (FSTAT) of the genetic substructure and gene flow patterns on a microgeographic scale. The results are discussed in the light of their relevance for the fixation process of chromosomal variants in *S. araneus*.

Garagna et al. (1989): Spermatogenesis in heterozygotes for Robertsonian chromosomal rearrangements from natural populations of the common shrew, *Sorex araneus*.
J.Reprod.Fert.87, 431-438

Wallace B.M.N. & Searle J.B. (1990): Synaptonemal complex studies of the common shrew (*Sorex araneus*).
Comparison of Robertsonian heterozygotes and homozygotes by light microscopy. Heredity 65, 359-367

The evolution of recombination under fluctuating selection: when is it possible?

Alexey S. Kondrashov and Lev Y. Yampolsky

We consider the evolution of recombination in a polymorphic population under fluctuating selection acting on one or many quantitative traits. Each of the traits is determined by a number of additive loci with two alleles that can mutate into one another. Another unlinked locus determined the rate of recombination between selection loci. We analyzed the outcome of selection acting in a population with two of the following alleles of the recombination locus present: 1) allele causing apomictic reproduction; 2) allele causing limited recombination between the loci influencing selection trait and 3) allele causing amphimixis with free recombination between loci. Amphimixis has a short-term advantage over apomixis if selection fluctuates frequently and widely, so that every genotype often has a low fitness. Such selection causes a significant load even in with amphimixis. The allele causing free recombination can have a significant advantage only if the rate of change of selection is such that the load is ~ 0.3 or more. If selection changes slower, an intermediate recombination rate can be established either due to fixation of allele that causes limited recombination or due to stable coexistence of alleles causing apomixis and amphimixis.

We conclude that fluctuating selection can be the factor responsible for short-term advantage of recombination only in the special conditions of frequent and strong changes of the environment.

420 The evolution of minicircles in trypanosomatids 72

Yurchenko, V. Yu., Kolesnikov, A.A.

Department of Molecular Biology, Moscow State University,
119899 Moscow, Russia

It is known, that kinetoplast DNA associates consist of minicircle molecules, that differently organized, e.g. molecules with various number of conservative regions (CRs). We are suppose that it is reflection of different evolution ranges of this organisms, because CR contains replication *ori* and this region is very useful for cell. We assume that, organisms with multi-CRs minicircles are more progress, than organisms with one-CR minicircles. As usually considerate, the minicircles within one associate are evolved independently. The populations of minicircles with different organization are one of "hot points" of trypanosomatids evolution.

But *in vivo* only one region functionate as replication *ori*, and other regions must be blocked. Possibly, the next step of evolution process is minicircles with pseudo-CRs plus one functional *ori*. As example, in *Trypanosoma brucei* and other trypanosomatids we can obtain a lot of modified universal dodecamers. In this occurrence cells do not synthesized the abundance of proteins for blocking, but in other conditions this regions may functionate as replication *ori*.

Our hypothesis is concorded with rRNA genes scheme of evolution for trypanosomatids.

The spread of a retrotransposon
in sexual and asexual populations of yeast.

The most plausible interpretation of the occurrence of transposable elements is that they spread infectiously when rare, irrespective of any other consequences they may have when they become abundant or domesticated. We transformed strains of yeast with the element Ty-3 and used the transformants to introduce it at low frequency into isogenic populations. The experimental populations varied in ploidy and in sexuality. Asexual populations were haploid or diploid. In either case, the element could be either activated or repressed through its linkage with a beta-galactosidase promoter. In sexual populations that went periodically through a haploid-diploid cycle of mating and sporulation, the element could be induced in the haploid phase, or in the diploid phase, or in both, or in neither. The leading result of the experiment was the rapid spread of the element in sexual populations and its loss from asexual populations, when transposition was induced by growth on galactose. This provides solid experimental support for the interpretation of transposable elements as genomic parasites. There were, however, two anomalous results. One was the spread of Ty-3 in some lines where transposition was repressed by growth on glucose. Its presence seems to be associated with a mating advantage in these cases. The second was the failure of Ty-3 to spread rapidly in sexual populations when transposition was induced in both the haploid and diploid phases. This was attributable to periodic selection for more efficient galactose utilization driving down the frequency of the rare Ty-3 - bearing lineages.

Insect Mitochondrial Control Region: Structure, Evolution and Usefulness in Evolutionary Studies

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T7

De-Xing Zhang & Godfrey M. Hewitt

Population Biology Sector, School of Biological Sciences,
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The control region (A+T-rich region) is the largest non-coding and presumably the most variable region in insect mitochondrial genome. Consequently, it has been regarded as an ideal DNA marker for detecting intraspecific polymorphisms. Comparative analyses of DNA sequences of this region from a diverse group of insects reveal several important characteristics: (1) A secondary structure element, probably associated with replication origin, is highly conserved in phylogenetically distant groups such as grasshoppers and *Drosophila*. Also, sequences flanking this stem and loop structure are highly conserved rather than sequence of the structure itself. (2) The control region in insects is extremely rich in A+T nucleotides, in most cases studied more than 86% (up to 96%) being A+T. (3) Conserved segments or short motifs can be identified between quite diverged taxa; the whole control region or its subdomains may be highly conserved between related species. (4) Mitochondrial control regions characterised in insect can be classed into 2 types, with type I containing clearly distinguishable conserved and variable domains, and type II without such division. Tandem repeats have been observed in both groups.

These characteristics have clear implications in use of this region in evolutionary studies. Firstly, the extreme A+T-rich composition of this region makes it very difficult to reveal polymorphisms with RFLP analysis, as few restriction enzymes are employable. Secondly, the frequent occurrence of tandem repetition in this region and length heteroplasmy hinder correct PCR amplification of the entire region and subsequent sequence analysis. It also seems that the control region does not evolve as fast as previously speculated and certainly much slower than neutral nuclear sequences in some cases studied. The above aspects indicate limitations for this region in intraspecific systematics studies, especially when PCR-sequencing is the main technique for detecting polymorphisms. However, for species with a tandem repeat-free control region, it may be useful for detecting polymorphism, if no other mitochondrial sequences reveal enough genetic variation. The existence of some highly conserved sequence motifs or segments within this region may allow one to design conserved PCR/sequencing primers to study closely related species. Finally, as widely conserved structural elements seem to exist across insect taxa in this major mitochondrial regulatory region, it will be most interesting to study the possible evolutionary processes involved.

CHROMOSOMAL EVOLUTION IN THE MAMMALS AND FISHES IN EUROPE

Jan Zima¹, Petr Ráb¹, Miloš Macholán¹, Ruth B. Phillips²

¹INSTITUTE OF ANIMAL PHYSIOLOGY AND GENETICS, CZECH ACADEMY OF SCIENCES, BRNO and LIBĚCHOV, CZECH REPUBLIC

²DEPARTMENT OF BIOLOGICAL SCIENCES, UNIVERSITY OF WISCONSIN, MILWAUKEE, USA

Comparative and population cytogenetic research of the European terrestrial mammals and freshwater fishes is synoptically surveyed, and the pattern of chromosomal divergence found in the both group is considered and compared. Polyploidy and unisexual reproduction represent significant mechanisms of karyotypic and genomic evolution in certain lineages of the fishes but these processes do not occur in the recent mammals. This gives an opportunity to evaluate the importance of these mechanisms in the repatterning of the karyotype, and to assess the impact of such changes on the evolutionary divergence potential within a lineage. The question of the adaptive role of chromosomal rearrangement is further raised in respect of the assumed coincidence of major environmental changes and accelerated rates of karyotypic evolution. Possible feedbacks between chromosomal constitution and selection at the organismal level are exemplified in relation to contrasting habitats and geographic distribution patterns in fish and mammalian populations or species. Salmonid fishes, soricid insectivores and muroid rodents are employed as models and examples to demonstrate the evolutionary issues under discussion.

LIST of DELEGATES

The name and address of each registered delegate is given, together with the number and session of their talk/poster. Abstracts are printed in alphabetical order, by presenter, in the previous section.

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Horak Peeter	University of Tartu TARTU	153	8
Horovitz Auguste	The Hebrew University of Jerusalem JERUSALEM		
Ingvarsson Par K	University of Umea UMEA	157	16
Jaarola Maarit	Uppsala University UPPSALA	158(P)	17
Jablonka Eva	Tel-Aviv University TEL-AVIV	159	11
Jager Coenraad R	University of Amsterdam AMSTERDAM	160	16
Jako Eena	Eotvos Lorand University BUDAPEST	161	7
James Avis Crews	University College London LONDON	162	11
Jenkins Glyn	University of Wales ABERYSTWYTH	163&164	2&12
Jiggins Chris	University College London LONDON	165	17
Johnstone Rufus A	University of Cambridge CAMBRIDGE	167	8
Jokela Jukka	Indiana University BLOOMINGTON	166	1
Jones Catherine	Aberdeen University ABERDEEN	168	7
Jonsson K Ingemar	Lund University LUND	169	8
Juan Carlos	University of East Anglia NORWICH		
Judson Olivia	Oxford University OXFORD	170	1

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Kawecki Tadeusz	University of Helsinki HELSINKI	172	10
Keightley Peter	University of Edinburgh EDINBURGH		
Keller Laurent	University of Lausanne LAUSANNE	173	8
Kennedy Cathy	Oxford University Press OXFORD		
King Vanessa E	University of Cambridge CAMBRIDGE	175	2
Kipling David	Western General Hospital EDINBURGH	176	13
Kirkpatrick Mark	University of Texas TEXAS	176a&177	8&11
Klaas Manfred	I.P.K. GAFERSLEBEN		
Klein Manfred	Federal Agency for Nature Conservation BONN	178(P)	3
Knoll Steffi	Universite de Neuchatel NEUCHATEL		
Koelewyn Hans P	University of Oulu OULU	180(P)	5
Koella Jacob	University of Aarhus ARHUS	179	10
Koh Hung Sun	Chungbuk University CHEONGJU	181	16
Koskela Esa	University of Jyväskylä JYRASKYTA	182	11
Kosuda Kazuhiko	Josai University SAITAMA	184(P)	4
Kotiaho Janne	University of Jyväskylä JYRASKYTA	185	8
Koufopanou Vassiliki	Imperial College at Silwood Park ASCOT		
Kovacs Rosie	Tensi Tours Congress Bureau BUDAPEST		

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Kover Ms Paula X	Indiana University BLOOMINGTON	187	14
Kozlowski Jan	Jagiellonian University KRAKOW		
Kraak Sarah B M	University of Bern HINTERKAPPELEN	189	9
Krleger Michael	Universite de Lausanne LAUSANNE - DORIGNY		
Kruuk Loeske E B	University of Edinburgh EDINBURGH	190a(P)	17
Kulttinen Helmi	University of Oulu OULU		
Kuke Bijlsma	University of Groningen HAREN		
Kuusipalo Liisa	University of Joensuu JOENSUU	192	7
Lachmann Michael	Stanford University STANFORD		
Lamb Marion J	LONDON		
Lampert Winfried	Max Planck Institute for Limnology PLOEN		
Lehmann Cornelia	University of Berlin BERLIN	194	4
Lenski Richard E	Michigan State University EAST LANSING	195	10
Leskinen Elina	Uppsala University UPPSALA	196(P)	7
Lessios Harilaos	Smithsonian Tropical Research Institut BALBOA		
Lindvall Anna	University of Uppsala UPPSALA		
Little Tom J	University of Guelph ONTARIO	197	1
Lively Curt	Indiana University INDIANA	198	1

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Loeschcke Volker	<i>University of Aarhus</i> AARHUS	199	16
Lomnicki Adam	<i>Jagiellonian University</i> KRAKOW	200	11
Lomonaco Cecilia	<i>University of Essex</i> ESSEX	201	11
Long Anthony D	<i>University of California at Davis</i> DAVIS	202	4
Lu Meng-Zhu	<i>Swedish University of Agricultural</i> UMEA	203	5
Lunadel Mario	<i>University La Sapienza</i> ROME	204(P)	2
Lundquist Elisabeth	<i>Umea University</i> UMEA		
Machado Carlos A	<i>University of California</i> IRVINE	205	2
Machkevsky Vladimir K	<i>Inst. of Biol. of Southern Seas</i> CRIMEA	206	14
Machon Nathalie	<i>Universite d'Orsay</i> ORSAY	207	5
Machordom Annie	<i>Subdirecciu General de Investigacion</i> ALCALA DE HENARES	208(P)	16
Mackay Trudy F C	<i>North Carolina State University</i> RALEIGH	209	4
MacKenzie Aulay	<i>University of Essex</i> COLCHESTER	210	8
MacKinnon Margaret	<i>University of Edinburgh</i> EDINBURGH	210a(P)	14
MacLean Valerie M	<i>Australian National University</i> CANBERRA CITY		
Mallet James	<i>Galton Laboratory</i> LONDON	212	17
Mangin Katrina	<i>University of Oxford</i> OXFORD		
Manning John	<i>University of Liverpool</i> LIVERPOOL	214	6

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Manolakou Katerine	Laboratoire Genome et Populations MONTPELLIER	214a	17
Mappes Tapio	University of Jyraskyta JYRASKYTA	216	11
Mappes Johanna	University of Jyraskyta JYRASKYTA	215	8
Marrow Paul	University of Cambridge CAMBRIDGE	219	8
Marshall Tristan	University of Edinburgh EDINBURGH		
Martin-Campos Jesus M	Universitat de Barcelona BARCELONA	220(P)	2
Martinez Juan Gabriel	University of Leicester LEICESTER	220a	8
Mason Philip	Universidad Autonoma de Madrid MADRID	221	13
Maurice Sandrine	Universite Montpellier II MONTPELLIER	222	9
Maxson Linda	The University of Tennessee KNOXVILLE	223	7
Maynard Smith John	University of Sussex BRIGHTON		
McCabe Jennie	University College London LONDON	224	4
McMillan W Owen	University College London LONDON	225	16
McWatters Harriet	University of Edinburgh EDINBURGH	225a	11
Meglecz Emese	KLTE DEBRECEN	228	16
Mes Ted H M	Utrecht University UTRECHT	229	7
Metz J A J	Leiden University LEIDEN	230	10
Michalakakis Ioannis	Universite Pierre & Marie Curie PARIS		

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Michiels Nico K	<i>Max-Planck-Institut SEEWIESEN</i>	233	9
Mignot Agnes	<i>Universite de Paris-Sud ORSAY</i>	234	6
Millinkovitch Michel C	<i>Free University of Brussels BRUSSELS</i>	235	7
Minelli Alessandro	<i>University Via Trieste PADOVA</i>	236	15
Mitchell Suzanne	<i>Max Planck Institute fur Limnologie PLOEN</i>	237(P)	1
Mokievsky Vadim O	<i>Institute of Oceanology MOSCOW</i>		
Moller Anders P	<i>Copenhagen University COPENHAGEN</i>	240	6
Moller Hansen Michael	<i>Inst. for Fisheries Research SILKEBORG</i>		
Montalvo Arlee	<i>University of California CALIFORNIA</i>	241(P)	16
Moritz Robin F A	<i>Institut fur Biologie BERLIN</i>	243	8
Mougel Florence	<i>Centre de Genetique Moleculaire CNRS GIF SUR YVETTE</i>	242(P)	16
Mouritsen Kim N	<i>University of Aarhus AARHUS</i>	244(P)	8
Muller Anthonie W	<i>University of Glasgow GLASGOW</i>		
Muller Christine	<i>Imperial College at Silwood Park ASCOT</i>		
Muller Jakob	<i>University of Mainz MAINZ</i>	245	17
Nagelkerke Cornelis J	<i>Imperial College at Silwood Park ASCOT</i>	246	8
Nauta Maarten	<i>State University HAREN</i>	247	9
Newton Adrian	<i>University of Edinburgh EDINBURGH</i>		

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Nielsen Einar Eg	University of Aarhus AARHUS	252(P)	16
Nishimura Kinya	Hokkaido University HAKODATE	253	8
Noach Estelle J K	Utrecht University UTRECHT	254	8
Noble Leslie R	Aberdeen University ABERDEEN	255	7
Nolrot Michel	Orston MONTPELLIER	256a	9
Nunney Leonard	University of California CALIFORNIA	257	16
Nurnberger Beate	University of Edinburgh EDINBURGH		
Nyakaana Silvester	University of Copenhagen COPENHAGEN		
Nyman Tommi	University of Joensuu JOENSUU	258(P)	3
O'Hara Bob	John Innes Centre NORWICH	261(P)	3
Ochando M Dolores	Universidad Complutense MADRID	259(P) 260(P)	16 16
Oka Nariko	Yamashina Institute for Ornithology CHIBA-KEN	262(P)	4
Okamura Beth	University of Bristol BRISTOL	263	1
Olivieri Isabella	Universite Montpellier II MONTPELLIER	264	16
Olsson Katarina	Umea University UMEA		
Onkamo Paivi	University of Helsinki HELSINKI	265(P)	2
Ottenheim Mart M	Inst. of Evolutionary & Ecol. Sciences LEIDEN	266	11
Otto Sarah	University of Edinburgh EDINBURGH	267	9

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Ouborg N Joop	University of Nymegen NYMEGEN	268	3
Palacios De La Cruz Carmen	University of Valencia VALENCIA	272(P)	7
Palo Jukka	University of Helsinki HELSINKI	270(P)	2
Palopoli Michael F	Howard Hughes Medical Institute ILLINOIS	269	4
Palsson Snaebjorn	University of Uppsala UPPSALA		
Pamilo Pekka	Uppsala University UPPSALA	271	16
Parri Silja	University of Jyvoskyllo KONNEVESI	274	8
Partridge Linda	University College London LONDON		
Pascoe Philip L	Plymouth Marine Laboratory PLYMOUTH	274a(P)	13
Pascual Marta	Universitat de Barcelona BARCELONA	275 276(P)	7 11
Passamonti Marco	University of Bologna BOLOGNA	277(P)	7
Paxton Robert	Uppsala University UPPSALA	280	8
Peck Joel R	The University of Sussex BRIGHTON	281	10
Pedersen Bo Vest	Zoological Institute COPENHAGEN		
Pemberton Josephine	University of Edinburgh EDINBURGH		
Pennington Toby	Royal Botanic Garden Edinburgh EDINBURGH	282	5
Perrin Nicolas	Lausanne University LAUSANNE	283	11
Petersen Petur H	University of Iceland REYKJAVIK		

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Petrie Marion	University of Oxford OXFORD		
Pettersson Tor Mikael	Umea University UMEÅ		
Plalek Jaroslav	The University of Edinburgh EDINBURGH	283a(P)	17
Polinsot Denis	Laboratoire de Dynamique du Genome PARIS	284	14
Popovkina Anastasya	Moscow State University MOSCOW	285a	8
Post Rory	Wageningen Agricultural University WAGENINGEN	286	7
Pouyaud Laurent	Universite Montpellier II MONTPELLIER	287	7
Price David J	University of Plymouth PLYMOUTH	288	13
Pritchard Jonathan K	Stanford University STANFORD	289	2
Prus-Glowacki Wieslaw	A Mickiewicz University POZNAN	290	5
Pulido Francisco	Max-Planck-Inst fur Verhaltensphysiol. RADOLFZELL	291	8
Pylkov Konstantin	Laboratory of Population Genetics MOSCOW		
Racey Ian	Imperial College at Silwood Park ASCOT		
Raijmann Leon E L	University of Amsterdam AMSTERDAM		
Ramsdale Mark	University of Bath BATH	293	9
Rand David A	University of Warwick COVENTRY	294	10
Rasmussen Ann-Sofie	Institute of Genetics LUND		

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Raymond Michel	Universite Montpellier II MONTPELLIER	295	6
Read Andrew	University of Edinburgh EDINBURGH	296	1
Reig Santiago	Museo Nacional de Ciencias Naturales MADRID	298 297	11 16
Renaud Sabrina	Universite Montpellier II MONTPELLIER	300	15
Repka Sari	Netherland Institute for Ecology NIEGWERSLGIS	301	11
Rey Isabel	Museo Nacional De Ciencias Naturales MADRID	302(P)	7
Rieseberg Loren H	Indiana University BLOOMINGTON	299	4
Rigaud Thierry	Universite de Poitiers POITIERS	303	14
Rispe Claude	INRA LE RHEU	304(P)	11
Ritchie Michael G	University of St Andrews ST ANDREWS	305	8
Roff Derek	McGill University MONTREAL	307	11
Ronfort Joelle	MAUGUIO	308	16
Rouhani Shamin	Sharif University TEHERAN		
Roy Michael S	University of Copenhagen COPENHAGEN		
Rublo Jose Miguel	Wageningen Agricultural University WAGENINGEN	311	17
Saether Bernt-Erik	NINA TRONDHEIM	312	8
Said Khaled	Faculte de Medecine Seutaine TUNISIA	313	13
Sandell Maria	Lund University LUND	314	8

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Sandmeier Michel	Universite de Paris-Sud ORSAY		
Sands David	Sycamores PRESTON		
Santucci Fiammetta	University of L'Aquila L'AQUILA	316	1
Sasaki Akira	Kyushu University FUKUOKA	315(P) 317	7 1
Saul George	Middlebury College VERMONT	318	14
Savolainen Outi	University of Oulu OULU	319&319a	4&16
Sbordoni Valerio	University of Rome ROME	320	7
Scali Valerio	University of Bologna PADOVA	321(P)	7
Scapoli Chiara	University of Ferrara FERRARA	322(P)	2
Schlerup Mikkel H	University of Aarhus AARHUS	323	16
Schilthuizen Menno	Wageningen Agricultural University WAGENINGEN	324	14
Schlotterer Christian	Zoology Institute MUNICH	358	2
Schmid Karl	University of Munich MUNICH	325	2
Searle Jeremy	University of York YORK		
Seitz Alfred	University of Mainz MAINZ		
Sella Gabriella	Department of Animal Biology TORINO	327(P) 328(P)	13 8
Sergeev Michael G	Novosibirsk State University NOVOSIBIRSK	329	16
Shanley Daryl	University of Manchester MANCHESTER		

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Sharpe Rosie	University of Leeds LEEDS	330	7
Sheldon Ben	Uppsala University UPPSALA	331	8
Shykoff Jacqui Anne	Institute of Technology ZURICH	332	14
Sih Andrew	University of Kentucky LEXINGTON	334	8
Simms Ellen L	University of Chicago CHICAGO	335	3
Simonsen Bo	University of Copenhagen COPENHAGEN		
Sinclair William	University of Edinburgh EDINBURGH	336	5
Skarsten Frode	University of Tromso TROMSO	337(P)	8
Smekens Marret J E	NIOO - CTO HETEREN	338(P)	11
Smith Henrik	Lund University LUND	339	8
Smithson Ann	University of Exeter EXETER	341	8
Soler Juan Jose	University of Copenhagen COPENHAGEN	341a	8
Sorci Gabriele	Universite Pierre & Marie Curie PARIS	342	11
Spitze Ken	University of Miami FLORIDA	343	11
Stadler Thomas	Universite Montpellier II MONTPELLIER	344	9
Stauffer Christian	University of East Anglia NORWICH	345(P)	7
Stearns Stephen	Zoology Institute BASLE	346	10
Stephan Wolfgang	BERLIN	347	2

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Stern David L	Cambridge University CAMBRIDGE	348	8
Stevens Jamie	The University of Bristol BRISTOL	349	7
Stevenson Ian	University of Edinburgh EDINBURGH		
Stewart Don	Dalhousie University NOVA SCOTIA	349a	7
Strahm Dora	University of Berne HINTERKAPPELEN		
Sugden Andrew M	Elsevier Science Ltd CAMBRIDGE		
Summers Anne	University of Essex COLCHESTER	350(P)	17
Sundstrom Liselotte	Bern University HINTERKAPPELEN	351	8
Svensson Erik	Department of Animal Ecology LUND	352	8
Svenstrup Michael	University of Aarhus AARHUS		
Swaddle John	University of Bristol BRISTOL	353	6
Szathmary Eors	Collegium Budapest BUDAPEST	354	12
Szmidt Alfred E	The Swedish University JMEA	355	5
Tanaka Yoshinari	McGill University QUEBEC	356	10
Taneyhill Dale	Universite Paris-Sud XI ORSAY		
Thomas Richard H	The Natural History Museum LONDON	360	1
Thomas Frederic	Universite Montpellier II MONTPELLIER	359	14
Thornhill Randy	University of New Mexico NEW MEXICO	361	6

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Thulin Carl-Gustaf	Uppsala University UPPSALA	362(P)	17
Till-Bottraud Irene	Universite Joseph Fourier GRENOBLE		
Tognola Maddalena	Universitat Bern HINTERKAPPELEN		
Tong Linda	Elsevier Trends Journals CAMBRIDGE		
Tristem Michael	Imperial College at Silwood Park ASCOT		
Ujhelyi Maria	Semmelweis University of Medicine BUDAPEST	365	8
Ulizzi Laura	University La Sapienza ROME	366(P)	16
Uotila Laura	University of Turku TURKU	367(P)	11
Ursing Bjorn M	Lund University LUND		
Vachot Anne-Marie	CNRS GIF SUR YVETTE	368(P)	7
Vakkari Pekka	Found HELSINKI	370(P) 369(P)	4 5
Valero Myriam	Universite de Lille VILLENEUVE D'ASCQ		
Van Baalen Minus	University of Warwick COVENTRY	371	10
Van Damme Jos	Netherlands Institute of Ecology HETEREN		
Van De Peer Yves	Universiteit Antwerpen ANTWERPEN	372(P) 373(P)	7 7
Van Delden Wilke	University of Groningen HAREN	374	4
Van Der Auwera Gert	Universiteit Antwerpen ANTWERPEN	375(P)	7
Van der Gaag Marijn	Agricultural University Wageningen DREIJENLAAN	376(P)	12

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Van Diepeningen Anne Dirkje	Agric. University Wageningen DREIJENLAAN	377(P)	14
Van Dijk Henk	Universite de Lille VILLENEUVE D'ASCQ		
Van Dijk Peter	NIOO C.O HETEREN	378(P)	1
Van Dooren Tom	University of Antwerp ANTWERPEN-WILRIJK	379	10
Van Hinsberg Arjen	Netherlands Institute for Ecology HETEREN	380	11
Van Rossum Fabienne	Free University of Belgium BRUSSELS	383	16
Van Tienderen Peter	Netherlands Institute for Ecology HETEREN	381	4
Vanlerberghe Flavie	I.N.R.A. ANTIBES	382	3
Vaughan Helen	UEA NORWICH		
Vekemans Xavier	Universite Libre de Bruxelles BRUSSELS	384	9
Verdyck Peter	Royal Belgian Institut of Nat. Sci. BRUSSELS	386(P)	1
Verhoog Michelle	Inst of Evolutionary & Ecol. Sciences LEIDEN	387	4
Vernon Jennifer	Genetics Laboratories OXFORD	388	1
Verra Federica	Universite de Rome ROME	389	17
Vieira Christina	Universite Claude Bernard-Lyon 1 VILLEURBANNE	390(P)	12
Villani Fiorella	Istituto per L'agroselvicultura PORANO	391	5
Visser Marcel E	Netherlands Institute of Ecology HETEREN	392	10
Vogl Claus	University of Veterinary Medicine AUSTRIA	393	8

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Volobouev Vitaly	<i>Institut Curie - Section de Biologie</i> PARIS	394	13
Volodin Serge	<i>Institute Biology of Southern Seas</i> SEVASTOPOL	395	16
Wallin Laura	<i>University of Helsinki</i> HELSINKI	398	8
Wall Richard	<i>The University of Bristol</i> BRISTOL	399	15
Wang Xiao-Ru	<i>The Swedish University</i> UMEA		
Warburton Peter	<i>Western General Hospital</i> EDINBURGH	400	13
Wattier Remi	<i>Laboratoire de Genetique et Evolution</i> VILLENEUVE D'ASCQ	401	9
Weber Anke	<i>Netherland Institute for Ecology</i> NIEGWERSLGIS	402	11
Wedekind Claus	<i>University of Bern</i> HINTERKAPELLEN	403	1
Weinzierl Rolf	<i>MPIV Seewiesen</i> SEEWIESEN	404	1
Weis Arthur E	<i>University of California</i> IRVINE	405	11
Wenger Remo	<i>University of Berne</i> BERNE	406	17
Wennstrom Anders	<i>University of Umea</i> UMEA	407	3
Werren John	<i>University of Rochester</i> ROCHESTER	408	14
West Stuart	<i>Imperial College at Silwood</i> ASCOT	409	8
White Dr Lee	<i>The Wildlife Conservation Society</i> LIBREVILLE	410	5
Whitlock Michael	<i>University of Edinburgh</i> EDINBURGH		
Wickings E Jean	<i>Centre International de Recherches</i> FRANCEVILLE		

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Wilkins Adam S	Company of Biologists Ltd CAMBRIDGE	411	6
Windig Jack J	University of Antwerp ANTWERPEN	412	11
Witting Lars	University of Aarhus AARHUS	413&414	8&10
Wolff Kirsten	University of St Andrews ST ANDREWS		
Wool David	Tel Aviv University TEL AVIV	416	3
Wuster Wolfgang	University of Wales BANGOR	417	7
Wyngaarden Pieter	University of Leiden LEIDEN		
Wyttenbach Andreas	Universite de Lausanne LAUSANNE - DORIGNY	418(P)	13
Yampolsky Lev	Russian Academy of Sciences MOSCOW	419	1
Zhang De-Xing	University of East Anglia NORWICH	422	7
Zima Jan	Institute of Animal Physiology BRNO	423	12

Timetable changes

Only those parts of the programme which have changed are shown

Plenary session (Wednesday, 08.30)

A discussion led by LR & TR Meagher, on *The emerging relevance of evolutionary biology to applied problems*

1) The Red Queen: selection for genetic diversity

Thursday

		<i>Chair: A Read</i>	<i>Ancient asexuals</i>
11.30 - 12.00	170	Judson OP	Preserving genes: the maintenance of genetic diversity in a model metapopulation
12.00 - 12.20	197	Little TJ & Hebert PDN	Cryptobiosis, the Red Queen, and the myth of the ancient asexual
12.20 - 12.40	360	Thomas R & Norton RA	Long-term parthenogenesis and the evolution of acariform mites
12.40 - 13.00	419	Kondrashov AS & Yampolsky L	The evolution of recombination under fluctuating selection: when is it possible?

Friday

		<i>Chair: D Ebert</i>	<i>Catching the Red Queen</i>
9.30 - 10.00	198	Lively CM, Jokela J & Dybdahl M	Through the looking glass: parasites sex and clonal diversity in a New Zealand snail
10.00 - 10.20	166	Jokela J & Lively CM	Parasites, sex and early reproduction in a mixed population of freshwater snails
10.20 - 10.40	296	Read AF, Morris K, Gemmill A & Viney ME	Is sexual reproduction by parasitic nematodes an immune evasion strategy?
10.40 - 11.00	137	Gulbrandtsen B	Variation in mating rate in hermaphrodites maintained by a sexually transmitted disease

Posters

72a	Cook M	The maintenance of sexual reproduction
237	Mitchell SE	Competition and the maintenance of genetic diversity in <i>Daphnia magna</i>
378	van Dijk P & Schotman T	The generation of genetic diversity in <i>Taraxacum officinale</i>
386	Verdyck P, Dsender K, Grootaert P & Hulselmans J	A comparison of genetic variability between mono- and polyphagous chrysomelid beetles of the genus <i>Phyllotreta</i> : a case study of the niche-width variation hypothesis

6) Developmental stability

Monday

		<i>Chair: AP Moller</i>	
		<i>Chair: AP Moller</i>	
16.00 - 16.20	295	Raymond M, Pontier D, Dufour AB & Moller AP	An evolutionary explanation for human handedness
16.20 - 16.40	353	Swaddle JP	Plumage condition affects flight performance in starlings: implications for developmental homeostasis, abrasion and moult
16.40 - 17.00	361	Thornhill R	Fluctuating asymmetry and honest signalling of phenotypic quality in human sexual selection
17.00 - 17.20	411	Wilkins AS	Gene families, partial functional redundancy and genetic stability
17.20 - 17.40	79	Dajoz I, Vincent M & Till-Bottraud I	Pollen heteromorphism, flower morphology and pollinator behaviour: a correlation.
17.40 - 17.50		Moller AP	Conclusion

7) Conflicting and concordant data sets in molecular systematics

Thursday			<i>Chair: R Post</i>	
12.30 - 13.00	330	Sharp P	Evolution of AIDS viruses	
Friday				
			<i>Chair: R Post</i>	
11.30 - 11.50	255	Noble LR, Jones CS, Vernon JG & Okamura B	A molecular and morphological investigation of the large arionids (Mollusca: Pulmonata) of NW Europe: identifying friend and foe	
11.50 - 12.10	192	Kuusipalo KL	Diversification of endemic Nile Perch <i>Lates niloticus</i> (Centropomidae, Pisces) populations in Lake Tanganyika, east Africa, studied with RAPD-PCR mtDNA evolution of neotropical pit vipers (<i>Bothrops atrox</i> species group)	
12.10 - 12.30	417	Wuster W & Salamao MG	Phylogenetic placement of the recently discovered Vu Quang ox based on multiple genetic loci	
12.30 - 12.50	123	Gatesy J & Arctander P		
Lunch				
			<i>Chair: R Crozier</i>	
14.00 - 14.20	76	Crozier RH, Dobric N, Imai HT, Graur D, Courmuet J-M & Taylor RW	Molecular phylogeny of the <i>Myrmecia pilosula</i> group, including ants with the lowest (possible) chromosome number	
14.20 - 14.50	103	Emerson BC & Wallis G	The systematics of the New Zealand flightless beetle genus <i>Prodontria</i> with some biogeographic and conservation implications	
14.50 - 15.10	211b	Malacrida AR, Guglielmino CR, D'Adam P, Torti C, Marinoni F & Gasperi G	Genetic analysis and phylogenetic inferences among species of Tephritid flies	
15.10 - 15.30	279	Paulauskas A, Sruoga A & Mozaliene E	Genetic variety and phylogeny of the Anseriformes order	
Tea				
			<i>Chair: R Crozier</i>	
16.00 - 16.20	349a	Stewart D, Hoeh R, Sutherland B & Zouros L	Accelerated rates of molecular evolution in the blue mussel, <i>Mytilus</i>	
16.20			<i>International Society of Biochemical Systematics business meeting</i>	

8) Behaviour and evolution

Tuesday		Chair: P Forslund	Parasitism
11.30 - 11.50	113	Forslund P	Intraspecific nest parasitism in the barnacle goose: behavioural tactics of parasites and hosts
11.50 - 12.10	348	Stern DL	Phylogenetic evidence that aphids, rather than plants, determine gall morphology
12.10 - 12.30	39	Bouludier T, Monnat J-Y & Danchin E	Ectoparasitism as a factor of habitat selection in a colonial bird
Lunch 13.00			

Posters

34	Blier P & Lemieux H	Energetic metabolism and habitat competition in <i>Nereis virens</i>
244	Mouritsen KN	Crawling behaviour in <i>Macoma balthica</i> : the parasite-manipulation hypothesis revisited
61a	Chapman T, Gray N & Partridge L	Nutrition, age at reproduction and the cost of mating in female <i>Drosophila melanogaster</i>
219	Marrow P, Stevenson IR, Clutton-Brock TH, Houston AI & McNamara JM	Reproductive decisions and life history tactics in Soay sheep
254	Noach EJK, de Jong G & Scharloo W	Locomotor activity in selection lines of <i>Drosophila melanogaster</i>
328	Sella G, Besostri Grimaldi B, Premoli MC & Ramella L	Sex ratio and local mate competition in <i>Dinophilus gyrocillatus</i>
112	Forchhammer MC & Boomsma JJ	Wait or wander: the evolution of mating system in musk oxen
341a	Soler JJ & Moller AP	Cuckoo host selection: characteristics determining the selection of the host by the European cuckoo (<i>Cuculus canorus</i>)
220a	Martinez JG, Soler M & Soler JJ	Egg destruction by great spotted cuckoos: adaptation or exaptation?
125	Gertsch P & Fjerdingstad EJ	Efficiency of detecting multiple inseminations in ants at different levels of sperm bias using microsatellite markers
133	Grootaert P	Male secondary sexual characters and sexual selection in the mawne fly genus <i>Cyrnatosus</i> (Insecta, Diptera, Dolichopodidae)
337	Skarstein F & Folstad I	On sperm and the immunocompetence handicap

14) Interactions between parasite transmission and sexual strategy

Thursday		Chair: P Kover	
16.00 - 16.30	332	Sheldon B	Evolutionary consequences of sexually transmitted diseases for host reproductive strategies
16.30 - 17.00	333	Shykoff J, Bucheli E & Kaltz O	Sexually transmitted plant diseases and attractive floral traits
17.00 - 17.20	155	Hurst G, Webberley M & Majerus M	Sexually transmitted disease in arthropods: an assessment
17.20 - 17.40	359	Thomas F, Renaud F, Demeus T, Cezilly F & Rouset F	Parasites, age and sexual selection
17.40 - 18.00	187	Kover PX & Clay K	RAPD markers indicate that horizontal transmission is the predominant mode of transmission in the mixed strategist <i>Atkinsonella hypoxylon</i>

15) Evolutionary radiations and development

Tuesday		<i>Chair: ENK Clarkson</i>	
9.30 - 10.00	3	Ahlberg PE	Conceptual leaps and morphological jumps: a coelacanth case study
10.00 - 10.30	23	Bateman RM	Explaining higher plant radiations: do radical developmental mutations drive phylogenetic change across fitness seascapes?
10.30 - 11.00	69	Clarkson ENK & Taylor CM	Heterochrony and evolutionary change in upper Cambrian Olenid trilobites
Coffee			
		<i>Chair: R Bateman</i>	
11.30 - 12.00	340	Smith AB	Evolutionary radiations in echinoderms: a comparison of larval and adult diversification
12.00 - 12.30	104a	Erwin DH, Valentine JW & Jablonski D	The developmental evolution of metazoan body plans: the fossil evidence
12.30 - 12.50	4	Alberch P	Exaptation and the intra-population and intra-specific evolution of viviparity in the urodele <i>Salamandra salamandra</i>
Lunch			
		<i>Chair: ENK Clarkson</i>	
14.00 - 14.20	300	Renaud S, Jaeger J-J & Auffray J-C	Uncoupled patterns of size and shape evolution in a fossil rodent (<i>Stephanomys</i>): a Fourier analysis approach
14.20 - 14.40	99	Eble GJ	Testing the role of development in evolutionary radiations
14.40 - 15.00	121	Galis F	New insights on a key evolutionary innovation
15.00 - 15.20	236	Fusco G & Minelli A	Morphological vs developmental complexity in centipedes
Tea			
		<i>Chair: R Bateman</i>	
16.00 - 16.20	399	Wall R & Stevens J	Radiation and classification of the blowfly genus <i>Lucilia</i> (Diptera: Calliphoridae)
16.20 - 17.00		<i>General discussion</i>	

16) Current topics in population structure

Thursday		<i>Chair: JKM Brown</i>	
16.00 - 16.20	124	Gentile G & Sbordoni V	A comparison of private alleles, G_{st} and θ for quantitative estimates of gene flow levels: <i>Andronisus dentiger</i> as a study case
16.20 - 16.40	257	Nunney L	The effective size of spatially structured populations
16.40 - 17.00	66	Cimmaruta R, Forti G, Nascetti G & Bullini L	Reproductive isolation and parapatric habitat displacement between the sibling species <i>Hydromantes ambrosii</i> and <i>H. strinati</i>