SIXTH CONGRESS
of the
EUROPEAN SOCIETY
for
EVOLUTIONARY BIOLOGY

24 - 28 August 1997

Arnhem, The Netherlands

PROGRAMME ABSTRACTS

ESEB VI

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Sixth Congress
of the
European Society
for
Evolutionary Biology

Arnhem, The Netherlands

24-28 August 1997

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Organisers

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CONTENTS

Programme:

Abstracts of Posters, Symposium talks, Contributed talks

INTRODUCTION AND OUTLINE OF THE CONGRESS

Welcome to the Netherlands and the Sixth Congress of the European Society for Evolutionary Biology. We hope that it will be a successful and inspiring meeting for all participants. We realize that the programme is very full, so in order to find your way easily we have tried to program the meeting as clearly and consistently as possible.

The first thing you probably want to know is when and where you are scheduled. The name index (p. 45) lists all Symposium organizers, Speakers, Poster presenters and Chairpersons. Co-authors are not listed, but they can be found in the abstracts. Abstracts of both talks and posters are in alphabetical order on the name of the presenting author. The line printed above an abstract also gives you the day and session. The abstracts of the plenary lectures can be found on page 49, before the other abstracts.

A concise schedule can be found on pages 6 and 7. All speakers are listed, which allows you to choose your session, mark the lectures you would like to see, and decide when to switch (or take a break..).

Each day starts with a plenary lecture by an invited keynote speaker, followed by five parallel symposia. Each symposium begins with three 30 minute lectures by invited speakers, and continues with contributed talks of 20 minutes (please allow 3 minutes for discussion). In addition to the symposia there are six afternoon sessions of contributed papers that did not fit in any of the symposia. The complete list of scheduled symposium- and contributed talks starts at page 12.

The Poster sessions are scheduled on Wednesday after lunch. The 16 parallel sessions start off with three minute presentations for each poster. After that, everyone is free to wander and look for the posters of his/her interest. Posters will be up, however, for most of the meeting, so we hope that this will give you ample time to study them. Poster locations are Room 2 and 3, and Foyer 3.

There are two days with a scientific evening programme: the Presidential Address and the John Maynard Smith prize winner's lectures on Sunday, and the ESEB Business meeting and Workshops on Monday. The other evenings are reserved for excursions, conference dinner and farewell party, respectively.

Posterboard for messages, announcements, job opportunities etc. will be provided in the Lobby, close to the Congress/Registration Desk.

THE NETHERLANDS INSTITUTE OF ECOLOGY

The Congress is hosted by the Netherlands Institute of Ecology (NIOO), Centre for Terrestrial Ecology at Heteren, approx. 20 km south of Papendal. The NIOO is a research institute of the Royal Netherlands Academy for Arts and Sciences and has three Centres. Research at the Centre for Terrestrial Ecology at Heteren focuses on terrestrial plant, micro-organism and animal populations, with special emphasis on the genetic strategies that help organisms adapt to changing environments. For instance, topics that are studied in the Department for Plant Population Biology are: the importance of sexual reproduction in plants, the evolution of phenotypic plasticity, and interactions between plant hosts and their pathogens. Study organisms include different Plantago species, Arabidopsis and its relatives, Silene, Taraxacum and Hordeum. The other departments of the Centre are the Department for Animal Population Biology (mainly focussing on the Great Tit and its prey species) and the Department for Plant Micro-organisms Interactions (studying the plants, nematodes and fungi in dunes, semi-natural grassland and disused farmland). Further information can be found on the website: **www.nioo.knaw.nl.** Many of the CTO people have been involved in making this meeting possible, for which they are gratefully acknowledged.

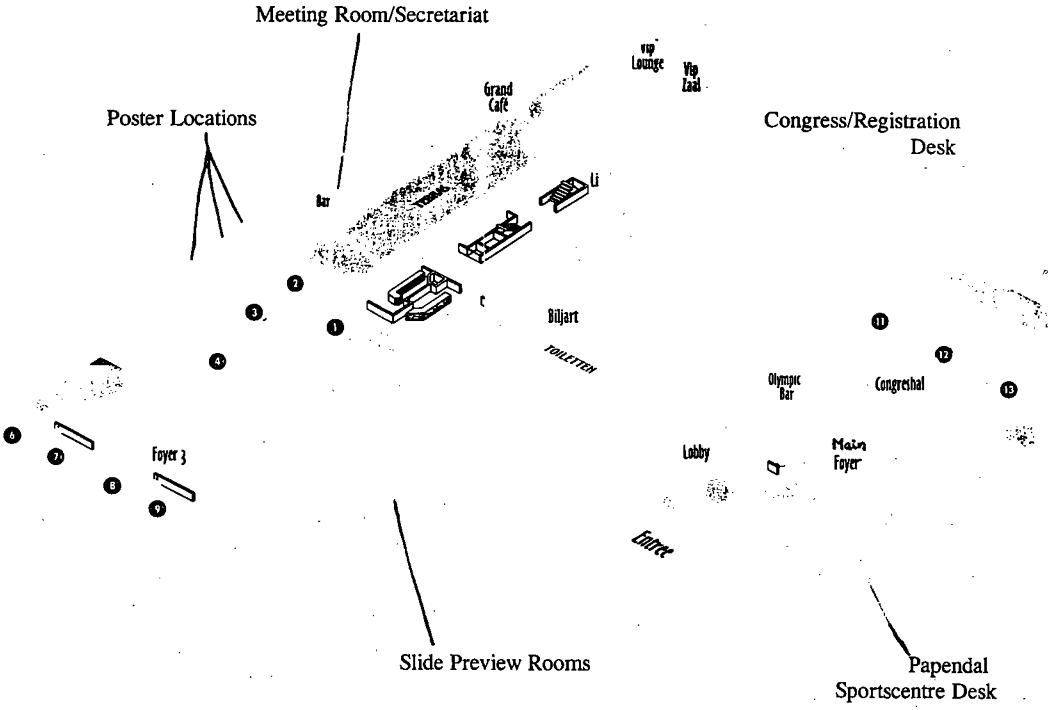
FINDING YOUR WAY AT PAPENDAL

MAP:

See map for the locations of the symposia and poster sessions.
The congress secretariat is in Room 1. The Preview rooms for slides are Room 10a and 10b.

Coffee and tea are served in the Main Foyer. All participants with lunch tickets can eat at Papendal, in the Restaurant on the first floor, or in the Main Foyer. Dinner tickets are either for Papendal or for West-End. Those with hotel accomodation at Papendal are welcome in the Papendal restaurant for dinner, starting at 18:30). Those with accomodation in the West-End motel can have dinner there. The restaurant of the motel is also open for non-residents. Other eating possiblities nearby are:

- Restaurant Pinoccio de Leeren Doedel, Amsterdamseweg 467, 6816 VK Arnhem. Tel. 026-3332344
  Italian and Dutch food; open from 17.00 onwards; approx 15 minutes walking from Papendal
- Various restaurants in the centre of Arnhem at 5-8 km distance from Papendal. You may ask for a list of restaurants at the Congress/Registration Desk



Lecture Rooms are
4+5
6+7
8+9
11
12+13

INSTRUCTIONS FOR AUTHORS

Preview facilities for slides are provided in Rooms 10a and 10b. You also can get a tray for your slides there. Give your tray to the projectionist in the break before your talk is scheduled. Immediately collect your slides and return the tray to the preview room after the session. For three slide projectors we have separate types of trays for thin (U.S.) and thick slides. However, the projectors in Rooms 11 and 12+13 may require remounting thin (U.S.) slides. **Speakers for symposia in Rooms 11 and 12+13 with thin slides are therefore requested to deliver their slides in the preview rooms at least three hours before the start of the session.**

Posters: Please put up your posters upon arrival, and remove the poster before Thursday afternoon. Posters are scheduled in 16 sessions. Sessions 1-5: Room 2; Sessions 6-10: Room 3; Sessions 11-16: Foyer 3. The name of the presenting author is indicated on the posterboard.

INSTRUCTIONS FOR CHAIRPERSONS

Chairpersons: Please check the index whether you are chairing a session of talks or posters.
Strictly adhere to the time schedule, please! Allow three minutes for discussion for all talks.
Those chairing a poster session: Give each presenter three minutes to highlight the main findings of the work.

ESEB SOCIETY MEETINGS

JEB Editorial Board:	Sat 23 Aug 20.00-22.00, Room 1
ESEB Officers & Council 1:	Sun 24 Aug 12.45-14.00, Room 1
ESEB Officers & Council 2:	Mon 25 Aug 12.45-14.00, Room 1
ESEB Business meeting (for all members of the society)	Mon 25 Aug 19.30-20.15, Room 12+13

DISPLAY OF PUBLISHERS AND OTHER COMPANIES

In the Main Foyer you will find displays of :

Wisepress, representing many of the world's leading publishing houses. All books on display can be ordered or bought directly at the stand. Free sample copies of journals are available on display.

Oxford University Press and **Blackwell Science** will present their current catalogue of books and journals, Blackwell will also demonstrate their Evolution CD ROM.

The Company **Noldus Information Technology** will demonstrate equipment for use in behavioural-ecological research on Thursday 28 August.

The **NIOO-CTO** will demonstrate recently developed equipment for fully automated silver-staining of sequence gels, which can be used for non-radioactive DNA detection in microsatellite, RFLP and SSCP techniques.

Congress ESEB97

Sat 23		
14:00-22:00		Arrival and registration
20:00-22.00	JEB Editorial Board Meeting in Room 1	

Sun.24	6+7	8+9	2+3	12+13	11
8:30-9:30				Brakefield	
	Evolution of Sexual and Social Systems	**Coevolutionary Interactions**	**Adaptation and Fitness**	**DNA and Evolution**	**Selection, Drift, and Evolution**
9:35-9:40	**S2 Sex determinatio**	**S8 Plant-Herbivores**	**S12 Plasticity**	**S20 Geographical pa**	**S24 Organism and M**
9:40:10:10	Bopp	Mattson	Dorn	Hewitt	Gorshkov, Victor
10:10:10:40	Werren	Strauss	Van Tienderen	Bachmann	Laland
coffee					
11.10-11:40	Saumitou-Laprade	Tuomi	Pigliucci	Nichols	Syvanen
11:40:12:00	Mittwoch	Weis	Sultan	Lenormand	Amabile-Cuevas
12:00-12:20	Kraak	Honkanen	Ottenheim	Nuernberger	Bulat
12:20-12:40	Antezana	Marak	Smekens	Mueller	Makarieva
lunch	12:45 -14:00 Meeting Council & Officers 1 in Room 1				
14:10-14.30	Rigaud	Janz	Gabriel	Cosson	Filatov
14:30-14:50	Beye	Egas	Van Straalen	Cianchi	Otto
14:50-15:10	Butcher	Kooi	Ernsting	Grandjean	Lenton
15:10-15:30	Gertsch	Biere	Martinez	Fedorov	Gorshkov, Vadim
15:30-15:50	Krieger	Desouhant	Repka	Alberch (Boto)	Sokolov
tea		**C2 Animal life h.**			**C4 Applic Molecular**
16:20-16:40	Van Dijk P.	Toupance	De Jong G.	Salemi	Gonzales-Candelas
16:40-17:00	Dikalova	Reuter	Gibert	Vandamme A.M.	Procaccini
17:00-17:20	De Jong T.	Johst	Roskam	De Haan	Launey
17:20-17:40	Vassiliadis	Spaak	Windig	Wolff, Kirsten	Desmarais
17:40-18:00			Wijngaarden	Dijkstra	Souty-Grosset
dinner					
20:00-20:45				**Stearns, Presidential Address**	
20:45-21:30				**Anstett, JMS lecture**	

Mon 25	6+7	8+9	2+3	12+13	11
8:30-9:30				Lenski	
	S4 Sexual selection	**S9 Symbiosis**	**S11 Plant life histori**	**S18 Microsatellites**	**S21 Conservation**
9:40:10:10	Zuk	Moran	Cohen	Pollock	Lande
10:10:10:40	Moller	Law	Schlichting	Ruiz Linares	Arctander
coffee					
11.10-11:40	Grahn	Douglas	Savolainen	Feldman	Avise
11:40:12:00	Kotiaho	Hackstein	Prus-Glowacki	Brunner	Bijlsma
12:00-12:20	Bakker	Van Hoek	Mathias	Falush	Van Oosterhout
12:20-12:40	Alatalo	Moya	Klinkhamer	Perrin	Gaggiotti
lunch	12.45-14.00 Meeting Council & Officers 2 in Room 1			**S20b Geographical p**	
14:10-14.30	Kokko	Van Ham	Ronce	Pongratz	Van de Zande
14:30-14:50	Webberley	De Vries	Piquot	Gerace	Saccheri
14:50-15:10	Parri	Breeuwer	Engel	Bjorklund	Nielsen
15:10-15:30	Hovi	Van Alphen	Atkinson	Merila	Santucci
15:30-15:50	Siva-Jothy	Bouchon	Vrieling	Kuusipalo	Vekemans
tea	**C3 Plant reproducti**		**C1 Bird Life History**		
16:20-16:40	Melser	Van Meer	Fauchald	Van Moorsel	Edmans
16:40-17:00	Velterop	Schilthuizen	Pulido	Verra	Siikamaki
17:00-17:20	Smithson	Scudo	Doutrelant	Brunton	Kuitinnen
17:20-17:40	Ferdy	Gibernau	Verboven	Post	Fischer
17:40-18:00		Gaume	Gavrilov		Hauser T.
18.15 dinner					
19:30-20:15	Plenary ESEB Business Meeting				
20:30-22:30	**Workshops W1 / W7**				

Tue 26	6+7	8+9	2+3	12+13	11
8:30-9:30				**Akam**	
9:35-9:40	**S1 Heteromorphism**	**S10 Genetic Conflict**	**S15 Microbial Evolut**	**S17 Modular vs Seg**	**S23 Domestication**
9:40:10:10	Till-Bottraud	Tristem	Riley	Dick	Kruska
10:10:10:40	Fenster	Nuzhdin	Chao	Spring	Ferrand
coffee					
11.10-11:40	Sachs	Ardlie	Dorit	Wray	Le Thierry d'Ennequin
11:40:12:00	Ressayre	Andersson	Blot	Boero	Allaby
12:00-12:20	Mignot	Hurst L.	Kulakov	Cook C.E.	Poncet
12:20-12:40	Joly	Cook J.M.	Rainey	Minelli	Tiedemann
12:40-13:00		McVean			
lunch					
13.45 -			**Excursions**		

Wed 27	6+7	8+9	2+3	12+13	11
8:30-9:30				**Jackson**	
9:35-9:40	**S5 Reproductive isol**	**S6 Parasite-host**	**S13 State-dependent**	**S16 DNA evolution**	**S25 Major Transition**
9:40:10:10	Hollocher	Richner	Shanley (Kirkwood)	Excoffier	Szathmary
10:10:10:40	Arnold	Agnew	Mace	Harding	Michod
coffee					
11.10-11:40	Tregenza	Lafferty	Verhulst	Sajantilla	Keller
11:40:12:00	Seehausen	Hochberg	Svensson	Schluens	Freeland
12:00-12:20	Aanen	Dupas	Cadee	Weiss	Bengtson
12:20-12:40	Trouve	Pomiankowski	Prevot-Julliard	Austerlitz	Brookfield
lunch					
14:10-15:00			**Parallel Poster sessions P1 / P16**		
15:00-15:50					
tea	**15.30 Film Joly**				
16:20-16:40	Kirkpatrick	Clay	Kozlowski	Nielsen	Kobayashi
16:40-17:00	Rolan Alvarez	Bauchau	Cichon	Chevillon	Noest
17:00-17:20	Michalak	Nash	Gotthard	Giessler	Sella
17:20-17:40	Ferguson	Flegr	Julliard	Barome	Witting
17:40-18:00	Schwarz (Leijs)	Rolff	Buckling	Aguade	Boxma

Conference dinner

Thu 28	6+7	8+9	2+3	12+13	11
8:30-9:30				**Piersma**	
9:35-9:40	**S3 Cooperation**	**S7 Parasitic disease**	**S14 Genet. fitness**	**S19 Exon-Intron**	**S22 Drift in natural p**
9:40:10:10	Komdeur	Levin	Keightley	Cerff	Charlesworth
10:10:10:40	De Waal	Koella	Chapman	Go	Barrett
coffee					
11.10-11:40	Ratnieks	Schmid-Hempel	Travisano	Stoltzfuss	Whitlock
11:40:12:00	Greeff	Kover	Turner	Dewilde	Kraft
12:00-12:20	Sundstrom	Kaltz	Korona	Hankeln	Caballero
12:20-12:40	Beekman	Van Baalen	Kammenga	Matthews	Palsson
lunch					
14:10-14.30	Seppa	Kraaijeveld	Davies	Da Lage	Giles
14:30-14:50	Heinze	MacKinnon	Leroi	Wolf, Klaus	Vitalis
14:50-15:10	Peeters	Slade	Betran	Haring	Armbruster
15:10-15:30	Sterck	Taskinen	Matos	Harlid	Wang
15:30-15:50	Kotenkova		Azevedo	Torti	Lenfant
tea		**C6 Predators/parasit**		**C5 Animal T/O**	
16:20-16:40	Hogendoorn	Bot	Blanckenhorn	Ahlroth	Schierup
16:40-17:00	Thoren	Pels	Ward	Crnokrak	Staedler
17:00-17:20	Pedersen	Frischknecht	Guillemaud	Verhoog	Gandon
17:20-17:40	Neumann	Jansen	Sabelis	Mappes	Heyer
17:40-18:00	Lachmann	Driessen	Lesna	Nordeide	Hardy
dinner					
Farewell party					

EXCURSIONS

Tuesday afternoon is the time for excursions. Except for the first, local excursion, transport by couch is included. Dinner will be somewhere on the road, and is not included in the NLG 35.- excursion fee. Good weather is not included in the fee either. Inquire at the desk whether tickets are still available. Note that excursions 3 (Batavia) and 5 (Palace het Loo) have been cancelled.

1. De Hoge Veluwe/Kröller-Müller

The National Park 'De Hoge Veluwe' is Holland's largest nature reserve with over 13,000 acres of woodland, heath, sand dunes and fens. It harbours many hundreds of red deer, mouflons, roes and wild boars. Situated in the Park are the 'Kröller-Müller' Museum (world-famous for its Van Gogh art collection and for works by Picasso, Mondriaan and others) and Europe's largest Sculpture Garden with works by Marta Pan, Hepworth, Rodin and many others. Bike rental and a guided tour through the Museum (starting at 15:00) is included in the fee.

- Bikes will be provided at the Papendal SportsCentre Tuesday at 13.45 and will have to be returned the same evening before 22.00. Please note that you will be held responsible for damage or loss of a bike and for returning the bike too late. Please be careful and lock the bike whenever you leave it unattended.

2. Burgers' Zoo, Arnhem

On an area of more than 45 hectares Burgers' Zoo houses over 3000 animals. Burgers' Zoo is specialised in anthropoid apes, particularly chimpanzees and gorillas, that have large natural territories. A brief introduction to the scientific research that takes place in the Zoo is scheduled. Burgers has a Safari-park with giraffes, zebras, rhinos and, of course, also lions and cheetahs. A spectacular tropical rain forest (the Bush) has been developed in a gigantic hall measuring 1.5 hectare, which houses exotic birds and many jungle animals. Finally, you can visit the replica of a North-American sub-tropical Desert.

- A bus will pick you up at Papendal at 13.45, and return at 22:00. Diner will be in nearby restaurants.

4. The Hanseatic town Zutphen

Seen from the west, the situation of Zutphen directly on the banks of the rivers IJssel and Berkel can not fail to impress. The centuries-old town received its town charter in 1190, and flourished during the 14th century as one of the towns belonging to the wealthy Hanseatic trading league. Its importance for travellers and residents at that time is reflected in the many monuments - from the imposing waterfront warehouses to the secluded and picturesque almshouses, interspersed with fragments of the town wall, church towers, town gateways and the 'Winehouse'. After a 45 minute bus ride a guided tour by foot is scheduled. You will have plenty of exploration time for yourself after that.

- A bus will pick you up at Papendal at 13.45, and return at 21.00. A list of restaurants in Zutphen will be provided.

6. Sports facilities at Papendal

As an alternative to the excursions, you may stay at Papendal on Tuesday afternoon and use the sports facilities. Look at the message board for information on the soccer tournament. Papendal is the National Sports Centre of the Netherlands, and has a range of in- and outdoor sports accommodations, such as a multi-functional sports-hall, a fitness-room, swimming pools, an 18-hole golf course (for those with an international licence), and facilities for soccer, tennis (bring your own racket), midget golf, petanque etc. You should book these facilities as early as possible, at the Sportscentre central desk (not the Congress desk). **Sport coordinator** for group activities will be Marcel Visser. One facility is free for those staying at the Papendal hotels: swimming before breakfast each day.

CONFERENCE DINER

The conference dinner Wednesday evening will be held in a traditional Farm House at the Dutch Open Air Museum. Typical buildings from 250 years of Dutch history, like old factories, wind mills and houses have been translocated from the Dutch provinces to the Museum, which are well worth seeing. We will leave in two groups. The busses will leave from Papendal at 19.00 and 20.00. There are no more tickets available (except perhaps on the black market...).

PLENARY LECTURES

All plenary lectures are in Lecture room 12+13

SUNDAY 24 AUGUST

8.30-9.30 Paul BRAKEFIELD (Leiden, The Netherlands)
The evolution of morphological diversity: genes and the development of eyespots

20.00-20.45 Stephen STEARNS (Basel, Switzerland)
Prediction of life histories and intrinsic mortality in evolutionary experiments
Presidential Address

20.45-21.30 John Maynard Smith Prize winner's lecture
Marie-Charlotte ANSTETT (Montpellier, France)
Facilitation and constraints in the evolution of mutualism?

MONDAY 25 AUGUST

8.30-9.30 Richard LENSKI (East Lansing, USA)
Adaptation and divergence during 10,000 generations of experimental evolution of E. coli

TUESDAY 26 AUGUST

8.30-9.30 Michael AKAM (Cambridge, United Kingdom)
Hox genes, homeosis and the evolution of segment identity

WEDNESDAY 27 AUGUST

8.30-9.30 Jeremy JACKSON (Balboa, Panama)
The tempo and mode of speciation revisited

THURSDAY 28 AUGUST

8.30-9.30 Theunis PIERSMA (Den Burg, The Netherlands)
Micro-evolution of shorebird migration patterns

MONDAY 25 AUGUST 20.30-22.30

If you are interested please sign up in the Main Foyer, near the registration desk. This is to find out the required room size for each workshop. The exact location will be posted Monday afternoon.

W1 Everybody Loves Evolution: pros and cons of popularising evolution
Organisers: Menno Schilthuizen (Wageningen, The Netherlands), Martin Enserink (Amsterdam, The Netherlands)

Over the past decade, evolution has reached unprecedented coverage in the media. As a result, its impact on society is increasing. For example, new insights into the evolution of human morality, language, sexuality, and disease are affecting our self-image. This workshop intends to have a closer look at these issues. We have invited the following four experts who occupy various positions along the line between evolutionary science and the public: exhibition designer Peter Koomen (Leiden Natural History Museum), science journalist Virginia Morell (journal Science), TV-producer Chris Hale (BBC-Television), popular science writer Robin "Sperm Wars" Baker.

W2 Evolution and natural biological regulation of the environment: the problem
Organisers: Victor Gorshkov (St-Petersburg, Russia), Anastasija Makarieva (St-Petersburg, Russia)

Environment on Earth changes, and this fact is often referred to as the first cause for evolution. Yet modern data show that natural biocommunities act against these changes and regulate their environment preserving it in a rather stable and favourable state.
What effect does it have on evolution? Is evolution to a certain degree suppressed? Is adaptation to changing environment the major mechanism of evolution? What is the alternative?

W3 Methodological approaches to spatial analyses
Organiser: Bryan Epperson (East Lansing, USA)

This workshop begins with descriptions of the conditions under which spatial versus space-time models and data may be used to infer population genetic processes. Some possible space-time models are presented, and various spatial statistics are reviewed. Following presentations, discussion is opened up to discuss other spatial methods and space-time models, for inferring rates of geneflow, strengths of selection processes, and determining the overall level of genetic variation among populations.

W4 Conservation genetics: molecular perspectives
Organiser: Lutz Bachmann (Tübingen, Germany)

This workshop is intended to discuss the status of Conservation Genetics in between ecology, genetics and required political decisions to protect endangered species and/or habitats. The discusssion will be chaired by Peter Arctander, Kopenhagen. Michel Milinkovitch, Brussels (Which type of molecular data for which kind of question?) and Russ Lande , Oregon, USA (Decisions in conservation genetics: Can we really rely on molecular data?) will open the discussion with two short introductory remarks.

W5 Is evolution by natural selection directional or not?

Organiser: Lars Witting (Aarhus, Denmark)

Since Darwin evolutionists have largely agreed that evolution by natural selection is a non-directional and deeply historical process. However, a new theory suggests that life-history evolution is a deterministically unfolding process in the way that a simple self-replicator in a stable and favourable environment automatically evolves towards the complex organisms on Earth. The arguments in favour of the two hypotheses will be explained, and a roundtable discussion will aim at identifying the scales at which the two hypotheses apply.

W6 Sex determination mechanisms in the order Hymenoptera

Organisers: Robert Butcher (Dundee, United Kingdom), Leo Beukeboom (Leiden, The Netherlands)

Sex determination in the order Hymenoptera (bees, wasps, ants, sawflies) appears to be ubiquitously based upon different forms of autosomal arrhenotoky (haplo-diploidy), with several independent evolutions of thelytokous partheneogenesis; but nothing is known at the molecular genetic level of how these mechanisms work or, consequently, have evolved. This workshop aims to draw together what is known so far from this and the related fields of microbial (e.g. Wolbachia) and b-chromosome (e.g. psr, sk, msr) sex determination or ratio distorters, and from sex determination in other orders or taxa to outline future research methods and models to enhance progress into the elucidation of the evolution and molecular genetics of Hymenopteran sex determination. People from all fields of interest are welcolme to participate.
Chairperson:- Robert Butcher (Dundee, UK); Introductary talks: Leo Beukeboom (Leiden, Netherlands); Richard Stouthamer (Wageningen, Netherlands); Jack Werren (Rochester, USA)

W7 Special interest roundtable on phenotypic plasticity

Organiser: Ariel Novoplansky (Ben-Gurion University, Sede-Boker Campus, Israel)

Since developmental moves take time, plastic development is often based on information regarding the probabilistic future rather than the current environmental conditions. Since this information is inherently limited, further plastic alternations are often utilized to fit the products of previous development to the eventual conditions. It is suggested that the study of phenotypic plasticity should focus the ways in which organisms process environmental information and execute developmental decisions based on partial and limited information, and correct them according to the changing conditions. Of special interest are the ecological and the evolutionary consequences of the functional and adaptive limitations of various classes of plasticity and the interchanging and compensatory interplay among them in organisms that are developing in constantly changing environments.
Participants are invited to raise open problems in phenotypic plasticity. Emphasis will be placed on questions of an interdisciplinary orientation.

Room:	6+7	8+9	2+3	12+13	11
	Evolution of Sexual and Social Systems	**Coevolutionary Interactions**	**Adaptation and Fitness**	**DNA and Evolution**	**Selection, Drift, and Evolution**
Sun 24	S2 Sex-determining mechanisms	S8 Plant-Herbivore relationships	S12 Phenotypic Plasticity	S20 Geographical Patterns	S24 Organism and its milieu
		C2 Animal life history			C4 Application Molecular markers
Mon 25	S4 Parasite-driven Sexual selection	S9 Symbiosis	S11 Plant life histories	S18 Microsatellites	S21 Genetics and Conservation
	C3 Plant reproductive biology		C1 Bird life Histories	S20b Geographical patterns (cont)	
Tue 26	S1 Heteromorphism	S10 Genetic Conflicts	S15 Microbial Adaptation	S17 Modular vs Segmented organisms	S23 Domestication and evolution
Wed 27	S5 Reproductive isolation	S6 Parasite/Host life cycles	S13 State-dependent life histories	S16 Evolution inferred from DNA	S25 Major Transitions
Thu 28	S3 Cooperation in animal societies	S7 Parasitic diseases	S14 Genetics of fitness in Model organisms	S19 Exon-Intron structures	S22 Drift in natural populations
		C6 Predators and parasites		C5 Trade Offs Animals	

SUNDAY 24 AUGUST LECTURE ROOM 6+7

Symposium S2 Evolution of sex-determining mechanisms

Organisers: Leo Beukeboom (Leiden, The Netherlands), Richard Stouthamer (Wageningen, The Netherlands)

Chair: Leo Beukeboom

9.35 Introduction

9:40 Daniel BOPP (Zürich, Switzerland)
The evolution of sex-determining mechanisms in Diptera

10:10 John WERREN (Rochester, USA)
Sex determination and genetic conflict

Chair: Richard Stouthamer

11:10 Pierre SAUMITOU-LAPRADE (Villeneuve d'Ascq, France)
Cytoplasmic male sterility in plants: molecular evidence and the nucleocytoplasmic conflict

11:40 Ursula MITTWOCH (London, United Kingdom)
Sex-determining mechanisms and the development of the dominant gonad in mammals and birds

12:00 Sarah KRAAK (Hinterkappelen, Switzerland)
Differential growth and the evolution of sex chromosomes: a simulation study

12:20 Marcos ANTEZANA (Chicago, USA)
Strong selection might have favored every step in the transition from diploid asexuality to one and two-step meiosis

Chair: Ursula Mittwoch

14:10 Thierry RIGAUD (Poitiers, France)
The evolution of sex determining mechanisms in isopod crustaceans: is the heterogamety evolution driven by genomic conflicts?

14:30 Martin BEYE (Berlin, Germany)
Validation of the sex locus concept in the honeybee using molecular data

14:50 Robert BUTCHER (Dundee, United Kingdom)
Whither the diploid males? A study of single locus complimentary sex determination in three Ichneumonid parasitoids across the UK

15:10 Pia GERTSCH (Uppsala, Sweden)
The load of diploid male production and the queen mating frequency in the ant Formica truncorum

15:30 Michael KRIEGER (Lausanne, Switzerland)
Triploidy in fire ants (Solenopsis invicta) associated with the polygyne social form

Chair: Robert Butcher

16:20 Peter VAN DIJK (Heteren, The Netherlands)
What makes a dandelion an apomict?

16:40 Anna DIKALOVA (Novosibirsk, Russia)
Polymorphism of mtDNA structure in sugar beet plants with normal and sterile cytoplasms of different origins

17:00 Tom DE JONG (Leiden, The Netherlands)
How geitonogamous selfing affects sex allocation in hermaphrodite plants

17:20 Christine VASSILIADIS (Villeneuve d'Ascq, France)
Estimation of incompatibility and relative male reproductive success at both pre-end postzygotic levels in the androdioecious Phillyrea augustifolia L.

SUNDAY 24 AUGUST LECTURE ROOM 8+9

Symposium S8 Evolution of plant-herbivore relationship: integration of biochemical, ecological and environmental aspects.

Organisers: Erkki Haukioja (Turku, Finland), Stig Larsson (Uppsala, Sweden)

Chair: Erkki Haukioja

9.35 Introduction (Haukioja)

9:40 W.J. MATTSON (Lansing, USA)
General plant defence theory: looking backward and forward

10:10 Sharon STRAUSS (Davis, USA)
The interplay between herbivory, pollination and plant reproductive traits

Chair: Stig Larsson

11:10 Juha TUOMI (Oulu, Finland)
Plant-herbivore interactions: antagonism versus mutualism?

11:40 Arthur WEIS (Irvine, USA)
The dimensions of selection on plant resistance: thinking beyond phytochemistry

12:00 Tuija HONKANEN (Edmonton, Canada)
Herbivory induced responses in plants: causes and consequences

12:20 Hamida MARAK (Heteren, The Netherlands)
The role of secondary plant compounds in defense against pathogenic fungi: costs and benefits iridoid glycosides

Chair: Arthur Weis

14:10 Niklas JANZ (Stockholm, Sweden)
The role of female search behaviour in determining host plant range in plant feeding insects: a test of the information processing hypothesis

14:30 Martijn EGAS (Amsterdam, The Netherlands)
Evolution in the greenhouse: a study on differential resistance to plant toxins in two races of a phytophagous mite.

14:50 Rinny KOOI (Leiden, The Netherlands)
Effects of food plant on wing pattern induction in the tropical butterfly Bicyclus anynana (Butler)

15:10 Arjen BIERE (Heteren, The Netherlands)
Host predisposition: effects of fungal infection of Silene alba on oviposition and performance of the noctuid Hadena bicruris

15:30 Emmanuel DESOUHANT (Villeurbanne, France)
Oviposition strategy and fitness in the chestnut weevil, Curculio elephas Gyll. (Coleoptera: Curculionidae)

Contributed Session C2 Animal Life History

Chair: Arie van Noordwijk

16:20 Bruno TOUPANCE (Orsay, France)
Genetic variations in aging cohorts

16:40 Max REUTER (Zürich, Switzerland)
The pattern of female arrival at the mating site in the yellow dung fly Scathophaga stercoraria represents a mixed ESS

17:00 Karin JOHST (Leipzig, Germany)
Evolution of dispersal: The impact of the temporal order of dispersal and reproduction within the life cycle

17:20 Piet SPAAK (Zürich, Switzerland)
Does fish predation facilitate co-existence in a Daphnia species complex?

17.40 Fjerdingstad

Symposium S12 The genetic basis of plasticity: what do we know and what do we wish to know?
Organisers: Massimo Pigliucci (Knoxville, USA), Carl Schlichting (Storrs, USA)

Chair: Massimo Pigliucci
9.35 Introduction (Schlichting)
9:40 Lisa DORN (Providence, USA)
The genetic basis of phenotypic plasticity: do plasticity genes exist or not?
10:10 Peter VAN TIENDEREN (Heteren, The Netherlands).
Genetic and environmental effects of character correlations under selection: what theory predicts and what Plantago does?

Chair: Carl Schlichting
11:10 Massimo PIGLIUCCI (Knoxville, USA)
How do we go about studying the genetic basis of plasticity?
11:40 Sonia SULTAN (Middletown, USA)
Phenotypic plasticity: defining the target of selection
12:00 Mart OTTENHEIM (Leiden, The Netherlands)
The evolution of plasticity in relation to phylogen
12:20 Marret SMEKENS (Heteren, The Netherlands)
Salt tolerance in Plantago coronopus: responses to artificial selection in constant and heterogeneous environments

Chair: Peter van Tienderen
14:10 Wilfried GABRIEL (München, Germany)
Evolution of reversible plastic responses: inducible defenses and environmental tolerance
14:30 Nico VAN STRAALEN (Amsterdam, The Netherlands)
Adaptive significance of Arrhenius activation energies estimated from temperature responses of ectotherm life-histories: the case of Collembola
14:50 Ger ERNSTING (Amsterdam, The Netherlands)
Intraspecific variation in temperature-reproduction relationships in ectotherms and its consequences for size and number of offspring
15:10 Enrique MARTINEZ (Santiago, Chile)
Growth response to a salinity gradient on microscopic stages of an intertidal kelp: a reaction norm approach
15:30 Sari REPKA (Nieuwersluis, The Netherlands)
Variation in filtering screens of Daphnia galeata: phenotypic adaptation to feeding conditions and genotypic differences

Chair: Massimo Pigliucci
16:20 Gerdien DE JONG (Utrecht, The Netherlands)
The evolution of reaction norms and density-dependent number regulation
16:40 Patricia GIBERT (Gif-sur-Yvette, France)
Genetics of phenotypic plasticity: body pigmentation in Drosophila.
17:00 Hans ROSKAM (Leiden, The Netherlands)
Wing pattern plasticity in Bicyclus: what factor triggers seasonal forms?
17:20 Jack WINDIG (Wilrijk, Belgium)
Genetic background of phenotypic plasticity in the European Map butterfly (Arascnia levana)
17:40 Pieter WIJNGAARDEN (Leiden, The Netherlands)
Selection on the slope of reaction norms for butterfly wing patterns

SUNDAY 24 AUGUST LECTURE ROOM 12+13

Symposium S20 Geographical patterns of intraspecific molecular variation
Organisers: Rory Post (Wageningen, The Netherlands), Valerio Sbordoni (Rome, Italy)

Chair: Rory Post
9.35 Introduction
9:40 Godfrey HEWITT (Norwich, United Kingdom)
Pleistocene effects on the distribution of genomes revealed by different DNA markers
10:10 Lutz BACHMANN (Tübingen, Germany)
Satellite DNA in Dolichopoda cave crickets: phylogeny versus geographic varation

Chair: Valerio Sbordoni
11:10 Richard NICHOLS (London, United Kingdom)
The limitations to what we can learn from geographic surveys of genetic differentiation
11:40 Thomas LENORMAND (Montpellier, France)
Estimating gene flow using selected markers: a case study
12:00 Beate NÜRNBERGER (München, Germany)
Indirect measures of selection on quantitative traits in hybrid zones
12:20 Jakob MÜLLER (Mainz, Germany)
Geographical patterns of nuclear and mitochondrial variation in two cryptic Gammarus types across a contact zone

Chair: Lutz Bachmann
14:10 Jean-Francois COSSON (Montpellier, France)
Comparative phylogeography and postglacial colonisation routes in Europe
14:30 Rossella CIANCHI (Roma, Italy)
Molecular phylogeography of European plethodeontid salamanders
14:50 Frédéric GRANDJEAN (Poitiers, France)
Genetic and morphological systematic studies of the species Austropotamobius pallipes (Decapoda: Astacidae)
15:10 Vadim FEDOROV (Uppsala, Sweden)
Mitochondrial DNA phylogeography and the evolutionary history of chromosome races of collared lemmings in the Eurasian Arctic
15:30 Pere ALBERCH (Madrid, Spain)
Molecular analysis of 'viviparous' and 'ovoviviparous' populations of Salamandra salamandra in Spain
(Abstract: see Luis BOTO)

Chair: Beate Nürnberger
16:20 Marco SALEMI (Leuven, Belgium)
Phylogentic identification of a possible origin of the human T-cell lymphotropic virus type II (HTLV-II) South European epidemics among injecting drug users (IDUs).
16:40 Anne-Mieke VANDAMME (Leuven, Belgium)
The three human T-cell lymphotropic virus type I subtypes arose from three geographically distinct simian reservoirs
17:00 Anita DE HAAN (Oulu, Finland)
Comparative genome mapping between Arabidopsis thaliana and Arabis petraea
17:20 Kirsten WOLFF (St. Andrews, United Kingdom)
Population differentiation of Plantago major
17:40 Eddy DIJKSTRA (Wageningen, The Netherlands)
Phylogeny and molecular evolution of Delphacid planthoppers

N.B. This symposium continues tomorrow, Monday, at 14:10, also in Lecture room 12+13

Symposium S24 The organism and its milieu: adaptation to or regulation of the environment
Organisers: Victor Gorshkov (St-Petersburg, Russia), Anastasija Makarieva (St-Petersburg, Russia), Sarah Otto (Vancouver, Canada)

Chair: Anastasija Makarieva
9.35 Introduction (Gorshkov)
9:40 Victor GORSHKOV (St-Petersburg, Russia)
Biological regulation of the environment: what is this and does it really exist?
10:10 Kevin LALAND (Cambridge, United Kingdom)
The evolutionary consequences of niche construction

Chair: Sergej Bulat
11:10 Michael SYVANEN (Davis, USA)
Horizontal gene transfer and patterns of Angiosperm evolution.
11:40 Carlos AMABILE-CUEVAS (Mexico, Mexico)
Bacterial plasmids, horizontal gene transfer and biological evolution
12:00 Sergey BULAT (Gatchina, Russia)
Species specific DNA: an open question
12:20 Anastasija MAKARIEVA (St-Petersburg, Russia)
Can evolution be explained without horizontal gene transfer?

Chair: Tim Lenton
14:10 Mickhail FILATOV (St-Petersburg, Russia)
Restriction of male fertility as a variant of natural selection mechanism for human population
14:30 Sarah OTTO (Vancouver, Canada)
The probability of fixation in populations of changing size
14:50 Tim LENTON (Norwich, United Kingdom)
The evolutionary biology of planetary self-regulation
15:10 Vadim GORSHKOV (St-Petersburg, Russia)
Community transformation of the environment: evidences and mechanisms of biotic regulation of the environment
15:30 Leonid SOKOLOV (St-Petersburg, Russia)
Mechanism of territory imprinting in birds

Contributed Session C4 Applications Molecular Techniques

Chair: Claire Brunton
16:20 Fernando GONZALEZ-CANDELAS (Burjassot, Spain)
The population structure of Limonium dufourii: a comparative analysis with RAPDs and AFLPs
16:40 Gabriele PROCACCINI (Napoli, Italy)
Microsatellite markers as a tool to investigate population genetic structure and gene flow in the endemic Mediterranean seagrass Posidonia oceanica
17:00 Sophie LAUNEY (La Tremblade, France)
Growth-heterozygozity relationship in oysters: new evidence from microsatellite markers
17:20 Erick DESMARAIS (Montpellier, France)
Direct detection of length polymorphisms (DDLP), or how to get new genetic markers in three days in any species.
17:40 Catherine SOUTY-GROSSET (Poitiers, France)
Molecular genetic approach in conservation of the white-clawed crayfish Austropotamobius pallipes pallipes

MONDAY 25 AUGUST LECTURE ROOM 6+7

Symposium S4 Parasite-driven sexual selection and the immunocompetence handicap hypothesis

Organisers: Frode Skarstein (Tromsø, Norway), Michael Siva-Jothy (Sheffield, United Kingdom)

Chair: Frode Skarstein
9.35 Introduction
9:40 Marlene ZUK (Riverside, USA)
Ornament expression and immune status
10:10 Anders Pape MØLLER (Paris, France)
Parasites, host immune defence, and host sexual selection

Chair: Michael Siva-Jothy
11:10 Mats GRAHN (Lund, Sweden)
Sexual selection and immunogenetic variation in the MHC
11:40 Janne KOTIAHO (Jyväskylä, Finland)
Costs of sexual traits
12:00 Theo BAKKER (Hinterkappelen, Switzerland)
Parasite transmission and its consequences for sexual selection in sticklebacks.
12:20 Rauno ALATALO (Jyväskylä, Finland)
Female choice for good genes- major benefits of minor costs?

Chair: Theo Bakker
14:10 Hanna KOKKO (Helsinki, Finland)
Is longevity a sexually selected trait?
14:30 Mary WEBBERLEY (Cambridge, United Kingdom)
Lack of evidence for parasite mediated sexual selection in ladybirds infected with a sexually transmitted parasite
14:50 Silja PARRI (Jyväskylä, Finland)
Small but significant benefits of female choosiness in a wolf spider?
15:10 Matti HOVI (Jyväskylä, Finland)
Hormonal responses of black grouse Tetrao tetrix males to the presence of competitors and females.
15:30 Michael SIVA-JOTHY (Sheffield, United Kingdom)
Immunocompetence and good genes.

Contributed Session C3 Plant Reproductive biology

Chair: Hans Koelewijn
16:20 Chantal MELSER (Leiden, The Netherlands)
Does Echium vulgare abort seeds selectively?
16:40 Odilia VELTEROP (Groningen, The Netherlands)
Gene flow in fragmented populations of insect-pollinated plants
17:00 Ann SMITHSON (Exeter, United Kingdom)
Deceptive pollination in Dactylorhiza sambucina
17:20 Jean-Baptiste FERDY (Paris, France)
Density-dependence of deceptive species reproductive success: population dynamics and conservation biology

MONDAY 25 AUGUST LECTURE ROOM 8+9

Symposium S9 The role of symbiosis in evolution
Organisers: Andres Moya (Valencia, Spain), Angela Douglas (York, United Kingdom)

Chair: Angela Douglas
9.35 Introduction (Moya)
9:40 Nancy MORAN (Tucson, USA)
The evolution of endosymbiosis in aphids
10:10 Richard LAW (York, United Kingdom)
The evolution of symbiotic structures: a theoretical framework

Chair: Andres Moya
11:10 Angela DOUGLAS (York, United Kingdom)
Why some animals have symbiotic micro-organisms
11:40 Johannes HACKSTEIN (Nijmegen, The Netherlands)
Methanogenic bacteria and anaerobic protists in the guts: evolutionary aspects
12:00 Angela VAN HOEK (Nijmegen, The Netherlands)
Evolutionary aspects of the symbiosis between anaerobic ciliates and methanogenic bacteria in the cockroach hindgut
12:20 Andres MOYA (Burjassot, Spain)
Evolution of the B-subunit of the F-ATPase complex in free living bacteria and Buchnera aphidicola, an aphid endosymbiont

Chair: Menno Schilthuizen
14:10 Roeland VAN HAM (Burjassot, Spain)
Evolution of amino acid biosynthetic pathways in Buchnera aphidicola, endosymbiont of aphids
14:30 Egbert DE VRIES (Amsterdam, The Netherlands)
Symbiotic bacteria in western flower thrips (Frankliniella occidentalis)
14:50 Hans BREEUWER (Amsterdam, The Netherlands)
Effects of Wolbachia symbionts on reproductive isolation and fitness of their spider mite host (Tetranychus urticae)
15:10 Jacques VAN ALPHEN (Leiden, The Netherlands)
The role of Wolbachia in cytoplasmic incompatibility in Trichopria arosophilae.
15:30 Didier BOUCHON (Poitiers, France)
Molecular phylogenies in the isopod-Wolbachia endosymbiosis

Chair: Johannes Hackstein
16:20 Marnix VAN MEER (Wageningen, The Netherlands)
ITS and 5SrRNA variation of different Wolbachia strains involved in sex-ratio distortion in arthropods.
16:40 Menno SCHILTHUIZEN (Wageningen, The Netherlands)
Selfish, shameless, and disloyal: Wolbachia's rise to success
17:00 Francesco SCUDO (Pavia, Italy)
Classic theories on symbiosis and evolution: Giglio-Tos and Kostitzin
17:20 Marc GIBERNAU (Montpellier, France)
The attraction of mutualistic pollinators by receptive figs of Ficus carica L.
17:40 Laurence GAUME (Montpellier, France)
To be or not to be mutualist? Comparison of two ant species inhabiting the same plant species

MONDAY 25 AUGUST LECTURE ROOM 2+3

Symposium S11 Evolution of plant life histories

Organisers: Subodh Jain (Davis, USA), Isabelle Olivieri (Montpellier, France)

Chair: Isabelle Olivieri
9.35 Introduction
9:40 Dan COHEN (Jerusalem, ISRAEL)
Modeling survival of stresses, and regeneration of damage in trees
10:10 Carl SCHLICHTING (Storrs, USA)
The role of phenotypic decisions in life history decisions

Chair: Dan Cohen
11:10 Outi SAVOLAINEN (Oulu, Finland)
Genetic variation in life history traits in Arabidopsis and relatives
11:40 Wieslaw PRUS-GLOWACKI (Poznán, Poland)
Relation between genetic structure and growth, survival and susceptibility to industrial pollution in forest tree populations.
12:00 Andea MATHIAS (Budapest, Hungary)
Evolutionary branching and coexistence of germination strategies
12:20 Peter KLINKHAMER (Leiden, The Netherlands)
The optimal timing of reproduction of semelparous perennials in temporally heterogeneous environments

Chair: Outi Savolainen
14:10 Ophélie RONCE (Montpellier, France)
Evolution of reproductive effort in a metapopulation
14:30 Yves PIQUOT (Villeneuve d'Ascq, France)
Life history evolution in Sparganium erectum: the consequences of metapopulation and local selection constraints
14:50 Carolyn ENGEL (Villeneuve d'Ascq, France)
The impact of the tri-phasic life history of red algae on the mating system: inbreeding and male gamete dispersal in Gracilaria gracilis
15:10 David ATKINSON (Liverpool, United Kingdom)
Sensitivity of plant developmental rate to non-vernalizing temperature: a theoretical analysis stimulated by observations on cereals
15:30 Klaas VRIELING (Leiden, The Netherlands)
Size dependent male reproductive success in a wind pollinated plant

Contributed Session C1 Bird Life History

Chair: Marcel Visser
16:20 Per FAUCHALD (Tromso, Norway)
On the cost of reproduction in longlived birds: the influence of environmental variability
16:40 Francisco PULIDO (Radolfzell, Germany)
Genetic correlations and microevolutionary trajectories of migratory behaviour in the backcap, Syliva atricapilla
17:00 Claire DOUTRELANT (Montpellier, France)
Trills in blue tit songs: a displaced character due to competition with great tit?
17:20 Nanette VERBOVEN (Heteren, The Netherlands)
Nest desertion and renesting behaviour in great tits
17:40 Valery GAVRILOV (Moscow, Russia)
Territoriality in birds: competition for better environment forms castes

MONDAY 25 AUGUST LECTURE ROOM 12+13

Symposium S18 Microsatellites - evolution and application
Organisers: Christian Schlötterer (Vienna, Austria), David Goldstein (Oxford, United Kingdom)

Chair: Christian Schlötterer
9.35 Introduction
9:40 David POLLOCK (London, United Kingdom)
Phylogeny reconstruction using microsatellites
10:10 Andres RUIZ LINARES (Medellin, Colombia)
Microsatellite variation in human populations

Chair: David Goldstein
11:10 Marcus FELDMAN (Stanford, USA)
Mutation models and evolution of microsatellites
11:40 Patrick BRUNNER (Zürich, Switzerland)
Comparative analyses of microsatellite and mtDNA markers: Holarctic differentiation in the Arctic charr (Salvelinus alpinus L.) complex
12:00 Daniel FALUSH (London, United Kingdom)
Microsatellite dynamics: evidence from genomic data
12:20 Niglas PERRIN (Lausanne, Switzerland)
Breeding system and genetic variance in the monogamous, semisocial shrew, Crocidura russula

Symposium S20 Continued

Chair: Rory Post
14:10 Norbert PONGRATZ (Starnberg, Germany)
Genetic diversity in sexual and parthenogenetic freshwater planarians, Dugesia polychroa, revealed by allozyme electrophoresis
14:30 Letizia GERACE (Starnberg, Germany)
Geographical patterns of genetic variation in,populations of Dugesia polychroa, a hermaphroditic planarian with sexual and parthenogenetic forms
14:50 Mats BJÖRKLUND (Uppsala, Sweden)
Shallow geographic structure in the greenfinch Carduelis chloris as revealed by microsatellites
15:10 Juha MERILÄ (Turku, Finland)
Historical demography of the greenfinch, Carduelis chloris- An analysis of mtDNA control-region sequences
15:30 Liisa KUUSIPALO (Joensuu, Finland)
Dynamic cluster analysis of binary RAPD data suggests differentation among endemic clupeid populations in Lake Tanganyika

Chair: Mats Björklund
16:20 Coline VAN MOORSEL (Leiden, The Netherlands)
Speciation patterns and ancestral distributions in Albinaria inferred from ITS Sequences
16:40 Federica VERRA (Roma, Italy)
Preliminary data on the molecular variation in Quercus Robur complex from peninsular Italy, Sardinia and Corsica
17:00 Clair BRUNTON (Cambridge, United Kingdom)
Mitochondrial DNA phylogeny of Brimstone butterflies (genus Goneptery) from the Canary Islands and Madeira
17:20 Rory POST (Wageningen, The Netherlands)
Are populations of the Simulium damnosum complex on the island of Bioko isolated from mainland immigration?

MONDAY 25 AUGUST LECTURE ROOM 11

Symposium S21 Genetics and conservation biology
Organisers: Kuke Bijlsma (Groningen, The Netherlands), Philip Hedrick (Tempe, USA)

Chair: Kuke Bijlsma
9.35 Introduction
9:40 Russ LANDE (Eugene, USA)
Genetic and demographic factors in extinction
10:10 Peter ARCTANDER (Copenhagen, Denmark)
Population genetic studies of African bovids - implications for conservation

Chair: Russ Lande
11:10 John AVISE (Athens, USA)
Conservation genetics: molecular perspectives
11:40 Kuke (R.) BIJLSMA (Haren, The Netherlands)
Environmental stress, detrimental alleles and extinction probability of small populations.
12:00 Cock VAN OOSTERHOUT (Leiden, The Netherlands)
On the consequences for conservation: stochasticity and genetics in metapopulations, a pedigree approach
12:20 Oscar GAGGIOTTI (Bangor, United Kingdom)
The effect of life-history schedule, recruitment failures, and fishing mortality on the effective population size of pelagic fish

Chair: John Avise
14:10 Louis VAN DE ZANDE (Haren, The Netherlands)
Effective population size of two bottlenecked Seychelles Warbler populations estimated from multilocus DNA fingerprint and demographic data
14:30 Ilik SACCHERI (Helsinki, Finland)
Heterozygosity and extinction in a butterfly metapopulation
14:50 Einar Eg NIELSEN (Aarhus, Denmark)
Analysis of microsatellite DNA from old scale samples of Atlantic salmon (Salmo salar L): a comparison of genetic composition over 75 years
15:10 Fiametta SANTUCCI (Norwich, United Kingdom)
Genetic structure and conservation biology of freshwater crayfish (Austropotamobius Pallipes) in Italy
15:30 Xavier VEKEMANS (Brussels, Belgium)
Conservation biology and multiallelic self-incompatibility systems: a story of partners and bachelors

Chair: Xavier Vekemans
16:20 Suzanne EDMANDS (Eugene, USA)
Inbreeding and outbreeding in an intertidal copepod: mate choice and fitness consequences
16:40 Pirkko SIIKAMAKI (Jyväskylä, Finland)
Development instability in Lychnis viscaria (L.) populations under genetic or environmental stress.
17:00 Helmi KUITTINEN (Oulu, Finland)
Genetic basis of inbreeding depression in Arabis petraea
17:20 Markus FISCHER (Zürich, Switzerland)
Plant performance in the rare Gentianella germanica in relation to population size, environmental and genetic (RAPD) variation
17:40 Thure HAUSER (Copenhagen, Denmark)
Fitness of hybrids between oilseed rape and weedy Brassica campestris: possibilities for introgression of transgenes from crops to wild species?

TUESDAY 26 AUGUST LECTURE ROOM 6+7

Symposium S1 Heteromorphism: intra-individual phenotypic polymorphisms
Organisers: Jacqui Shykoff (Paris, France), Isabelle Dajoz (Paris, France)

Chair: Jacqui Shykoff
9.35 Introduction (Shykoff)
9:40 Irene TILL-BOTTRAUD (Grenoble, France)
Heteromorphism of cyanogenesis in white clover: one way of reducing the costs of plant defence against herbivory
10:10 Charles FENSTER (College Park, USA)
Floral heteromorphisms: adaptive significance and developmental mechanisms underlying their evolution

Chair: Isabelle Dajoz
11:10 Tsvi SACHS (Jerusalem, Israel)
Phenotypic plasticity within individuals
11:40 Adrienne RESSAYRE (Orsay, France)
Pollen heteromorphism: developmental models of meiotic cytokinesis for the production of multiple phenotypes
12:00 Agnès MIGNOT (Montpellier, France)
Pollen aperture number heteromorphism: the problem of the origin
12:20 Dominique JOLY (Gif-sur-Yvette, France)
Sperm heteromorphism: sexual conflict for the control paternity

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TUESDAY 26 AUGUST LECTURE ROOM 8+9

Symposium S10 Genetic conflicts
Organiser: Austin Burt (Ascot, United Kingdom)

Chair: Austin Burt
9.35 Introduction (Burt)
9:40 Michael TRISTEM (Ascot, United Kingdom)
Retroviral evolution and distribution in the vertebrates
10:10 Sergey NUZHDIN (Davis, USA)
Host-retrotransposon coevolution in Drosophila

Chair: Austin Burt
11:10 Kristin ARDLIE (Cambridge, USA)
Selection on t haplotype chromosomes in natural populations of house mice (Mus musculus domesticus)
11:40 Helene ANDERSSON (Lund, Sweden)
Mitochondrial plasmids in Silene vulgaris
12:00 Laurence HURST (Bath, United Kingdom)
Evidence for a selectivily favourable reduction in the mutation rate of the rodent X chromosome
12:20 James COOK (Berkshire, United Kingdom)
Transposons as clade markers for their hosts
12:40 Gilean McVEAN (Cambridge, United Kingdom)
Testing the conflict theory of genomic imprinting

TUESDAY 26 AUGUST LECTURE ROOM 2+3

Symposium S15 Mechanisms and processes of microbial adaptation

Organisers: Margaret Riley (Yale, USA), Robert Dorit (Yale, USA)

Chair: Margaret Riley

9.35 Introduction

9:40 Margaret RILEY (New Haven, USA)
Molecular evolution of microbial defense systems

10:10 Lin CHAO (College Park, USA)
The evolution of sex and the molecular clock in RNA viruses

Chair: Robert Dorit

11:10 Robert DORIT (New Haven, USA)
In vitro evolution: adaptation at the molecular level.

11:40 Michel BLOT (Grenoble, France)
IS elements and genetic diversity during 10,000 generations of experimental evolution with Escherichia coli

12:00 Yuri KULAKOV (Moscow, Russia)
Adaptive acid tolerance response of Brucella

12:20 Paul RAINEY (Oxford, United Kingdom)
Ecological complexity and the maintenance of genetic variation

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TUESDAY 26 AUGUST LECTURE ROOM 12+13

Symposium S17 Modular versus segmented organisms

Organisers: Alessandro Minelli (Padova, Italy), Ferdinando Boero (Leece, Italy)

Chair: Alessandro Minelli

9.35 Introduction (Minelli)

9:40 Matthew DICK (Middlebury, USA)
Developmental commonality in annelid segments and bryozoan modules: a heuristic approach

10:10 Jürg SPRING (Basel, Switzerland)
Homeobox containing genes in the life cycle of cnidarians

Chair: Ferdinando Boero

11:10 Gregory WRAY (Stony Brook, USA)
Evolution of echinoderm body archtecture: from molecules to metamerism

11:40 Ferdinando BOERO (Lecce, Italy)
The cnidarian premises of metazoan evolution: from triploblasty, to coelom formation, to metamery

12:00 Charles COOK (Cambridge, United Kingdom)
Homeobox genes in the collembolan Folsomia candida

12:20 Alessandro MINELLI (Padova, Italy)
Geophilomorph centipedes as a model for the study of segmentation

12:40 Closing remarks (Boero)

TUESDAY 26 AUGUST LECTURE ROOM 11

Symposium S23 Domestication as approach to mechanisms of evolution

Organisers: Günther Hartl (Kiel, Germany), Ralph Tiedemann (Kiel, Germany)

Chair: Günther Hartl

9.35 Introduction

9:40 Dieter KRUSKA (Kiel, Germany)
The evolutionary implications of brain size reduction during domestication

10:10 Nuno FERRAND (Porto, Portugal)
Molecular variation within and among rabbit populations: effects of domestication

Chair: Robin Allaby

11:10 Maud LE THIERRY D'ENNEQUIN (Orsay, France)
Plant domestication: a stochastic model for understanding the influence of the reproduction mode, gene flow and drift on gene organisation

11:40 Robin ALLABY (Manchester, United Kingdom)
Domestication of Wheat (Triticum) in the Middle East, evidence from High Molecular Weight Glutenin Subunit Genes

12:00 Valerie PONCET (Orsay, France)
Domestication process in pearl millet (Pennissetum glaucum) : assessment of the genetic organisation

12:20 Ralph TIEDEMANN (Kiel, Germany)
The occurrence of tuskless bulls in Asian elephants (Elephas maximus) under natural vs. artificial selection conditions

Symposium S5 The evolution of reproductive isolation
Organisers: Steph Menken (Amsterdam, The Netherlands), Peter van Dijk (Heteren, The Netherlands)

Chair: Peter van Dijk
9.35 Introduction
9:40 Hope HOLLOCHER (Princeton, USA)
Unraveling genetic patterns of postmating reproductive isolation -- Haldane's Rule or Haldane's Coincidence?
10:10 Michael ARNOLD (Athens, USA)
Gene flow and natural selection in Louisiana irises

Chair: Steph Menken
11:10 Tom TREGENZA (Leeds, United Kingdom)
Signal divergence and reproductive isolation in a grasshopper
11:40 Ole SEEHAUSEN (Leiden, The Netherlands)
Intraspecific mate preferences based on a single locus colour trait in a cichlid fish.
12:00 Duur AANEN (Wijster, The Netherlands)
Reproductive isolation in the genus Hebeloma
12:20 Sandrine TROUVÉ (Perpignan, France)
Evidence of hybrid dysgenesis in a platyhelminth parasite

14:10-15.50 POSTER SESSION

15.30-15.50 Film
Love songs and Drosophila: evolution of dialects in D. teissieri
Presentation: Dominique JOLY (Gif-sur-Yvette, France)

Chair: Peter van Dijk
16:20 Mark KIRKPATRICK (Austin, USA)
A genetic model for reinforcement of mating preferences on an island
16:40 Emilio ROLAN ALVAREZ (Vigo, Spain)
Prezygotic mechanisms of incipient speciation in Littorina saxatilis (Gastropoda: Prosobranchia)
17:00 Pawel MICHALAK (Kraków, Poland)
Tests for sexual isolation between two newt species, Triturus vulgaris and T. montandoni
17:20 Willem FERGUSON (Pretoria, South Africa)
Geographic variation in the sound producing wing structures of field crickets Gryllus bimaculatus: consequences for speciation theory.
17:40 Michael SCHWARZ (Adelaide, Australia)
Radiation in some subgenera of large carpenter bees in relation to their mating system
(Abstract: see Remko LEIJS)

WEDNESDAY 27 AUGUST LECTURE ROOM 8+9

Symposium S6 Interactions between parasite life-cycles and host life-histories
Organisers: Jacob Koella (Aarhus, Denmark), Yannis Michalakis (Paris, France)

<u>Chair: Jacob Koella</u>
9.35 Introduction
9:40 Heinz RICHNER (Hinterkappelen, Switzerland)
Host-parasite interactions and the evolution of clutch size
10:10 Philip AGNEW (Aarhus, Denmark)
Environmental variation and life history interactions in a host-parasite relationship

<u>Chair: Yannis Michalakis</u>
11:10 Kevin LAFFERTY (Santa Barbara, USA)
If the shoe fits, wear it: the influence of host life history on parasite life history
11:40 Michael HOCHBERG (Paris, France)
Hide or fight? The competitive evolution of concealment and encapsulation in host-parasitoid assocations
12:00 Stephane DUPAS (Gif Sur Yvette, France)
Geographic variation in rates of immune reaction in a Drosophila-parasitoid system: the genetic and physiological mechanisms involved and the evolutionary forces operating.
12:20 Andrew POMIANKOWSKI (Berlin, Germany)
Why do hosts accept cuckoo chicks?

14:10-15.50 POSTER SESSION

<u>Chair: Heinz Richner</u>
16:20 Keith CLAY (Bloomington, USA)
Pathogens and plant life histories
16:40 Vincent BAUCHAU (Heteren, The Netherlands)
Why do pied flycatchers have fewer parasites than great tits?
17:00 David NASH (Hinterkappelen, Switzerland)
Mutualists on the edge, or why are there so few parasites?
17:20 Jaroslav FLEGR (Praha, Czech Republic)
Causality relationships between changes in human personality and Toxoplasma gondii infection. Manipulation or an epidemiological risk factor?
17:40 Jens ROLFF (Braunwscheig, Germany)
Better hosts dive: the life-cycle of ectoparasitic water mites and the interaction with the oviposition behaviour of their damselfly hosts

WEDNESDAY 27 AUGUST   LECTURE ROOM 2+3

Symposium S13 State-dependent life histories
Organisers: John McNamara (Bristol, United Kingdom), Alasdair Houston (Bristol, United Kingdom)

Chair: Simon Verhulst
9.35 Introduction
9:40 Daryl SHANLEY (Manchester, United Kingdom)
Optimal investment in maintenance as a function of physiological state
(see abstract under KIRKWOOD).
10:10 Ruth MACE (London, United Kingdom)
When to have another baby: wealth inheritance and reproductive decision-making in humans

Chair: Ruth Mace
11:10 Simon VERHULST (Haren, The Netherlands)
Energetics, immune function, and trade-offs in evolutionary ecology
11:40 Erik SVENSSON (Lund, Sweden)
Parental workload, immunocompetence and the energetic costs of immune responses
12:00 Niels CADÉE (Paris, France)
Developmental stability and physiological condition of barn swallows Hirundo rustica (L.) during the breeding season
12:20 Anne-Caroline PREVOT-JULLIARD (Oslo, Norway)
Cost of reproduction of female bank voles Clethrionomys glareolus in north Finland

14:10-15.50 POSTER SESSION

Chair: Erik Svensson
16:20 Jan KOZLOWSKI (Kraków, Poland)
Energy allocation between growth and reproduction: the Pontryagin Maximum Principle solution for the case of age- and season-dependent mortality
16:40 Mariusz CICHON (Kraków, Poland)
State dependent allocation to growth, reproduction and repair
17:00 Karl GOTTHARD (Stockholm, Sweden)
Seasonal plasticity in two butterflies: The effect of seasonal state on reaction norms relating life history traits to photoperoid
17:20 Romain JULLIARD (Oslo, Norway)
Density-dependent survival of adult and sub-adult multimammate rats
17:40 Angus BUCKLING (Edinburgh, United Kingdom)
Adaptive changes in Plasmodium life histories in response to intervention strategies

WEDNESDAY 27 AUGUST   LECTURE ROOM 12+13

Symposium S16 Evolution of populations inferred from DNA
Organisers: Arndt von Häseler (Munich, Germany), Svante Paabo (Munich, Germany)

Chair: Arndt von Häseler
9.35 Introduction (Von Häseler)
9:40 Laurent EXCOFFIER (Accacias, Switzerland)
The effect of mutational hot-spots on mtDNA sequence polymorphism.
10:10 Rosalind HARDING (Oxford, United Kingdom)
The ancestry of modern humans: inferences on gene trees for ß-globin sequences

Chair: Rosaling Harding
11:10 Antti SAJANTILLA (Helsinki, Finland)
Mitochondrial DNA analysis in Eurasian populations
11:40 Helge SCHLÜNS (Berlin, Germany)
A model of neutral evolution in haplo-diploid populations
12:00 Gunter WEISS (München, Germany)
The spread of agriculture in Eurasia as revealed by mtDNA sequences
12:20 Frédéric AUSTERLITZ (Orsay, France)
The impact of special demographic behaviour in a human population on allelic and haplotype frequencies and its consequences on the estimation of demographic and genetic parameters

14:10-15.50 POSTER SESSION

Chair: Arndt von Häseler
16:20 Rasmus NIELSEN (Berkeley, USA)
Maximum likelihood estimation of populations divergence times
16:40 Christine CHEVILLON (Montpellier, France)
A comparison of mtDNA control region sequences and their restriction polymorphism for native Panamanians and Mongolian
17:00 Sabine GIESSLER (München, Germany)
Reticulate evolution among species of the Daphnia longispina group
17:20 Pierre-Olivier BAROME (Gif-sur-Yvette, France)
Phylogenetic relationships within the genus Acomys (Rodentia, Muridae, Murinae): investigations using cytochrome b gene anlysis
17:40 Montserrat AGUADÉ (Barcelona, Spain)
Molecular evolution of the Cecropin multigene family in Drosophila: functional genes vs pseudogenes

Symposium S25 The major evolutionary transitions
Organisers: Eörs Szathmáry (Budapest, Hungary)

Chair: Eörs Szathmáry
9.35 Introduction
9:40 Eörs SZATHMARY (Budapest, Hungary)
The origin of the genetic code
10:10 Richard MICHOD (Tucson, USA)
Evolution of individuality

Chair: Eörs Szathmáry
11:10 Laurent KELLER (Lausanna, Switzerland)
The origin of insect societies
11:40 Stephen FREELAND (Cambridge, United Kingdom)
Hidden optimality of the genetic code
12:00 Bengt BENGTSSON (Lund, Sweden)
An upper limit to the size of genomes
12:20 John BROOKFIELD (Nottingham, United Kingdom)
Quorum sensing, group selection and multicellularity

14:10-15.50 POSTER SESSION

Chair: Bengt Bengtsson
16:20 Ichizo KOBAYASHI (Tokyo, Japan)
Evolution of sex: anti-genomic-parasite hypothesis
16:40 André NOEST (Utrecht, The Netherlands)
Instability of the sexual continuum
17:00 Guy SELLA (Tel-aviv, Israel)
Homeostatic mechanisms in the evolution of early development
17:20 Lars WITTING (Aarhus, Denmark)
The major transitions as a deterministically unfolding process
17:40 Brigitte BOXMA (Nijmegen, The Netherlands)
Chaperonine Hsp60 and Hsp70 encoding genes in anaerobic chytrids

THURSDAY 28 AUGUST LECTURE ROOM 6+7

Symposium S3 Co-operation in animal societies

Organisers: Jürgen Heinze (Nürnberg, Germany), Laurent Keller (Lausanne, Switzerland)

Chair: Jürgen Heinze/Laurent Keller

9.35 Introduction

9:40 Jan KOMDEUR (Melbourne, Australia)
Parent offspring conflict over sex ratio bias in co-operatively breeding vertebrates

10:10 Frans DE WAAL (Atlanta, USA)
The marketplace of social services in primates: simple and complex mechanisms of reciprocity

Chair: Elisabeth Sterck

11:10 Francis RATNIEKS (Sheffield, United Kingdom)
Conflict and reproductive manipulation in insect societies

11:40 Jaco GREEFF (Starnberg, Germany)
Female co-operation in Allodapine bees seen from a class structured perspective: evolution of sex ratios and colony sizes

12:00 Liselotte SUNDSTRÖM (Helsinki, Finland)
Fluctuating paternity and sex ratio biasing in the ant Formica truncorum

12:20 Madeleine BEEKMAN (Amsterdam, The Netherlands)
Bumblebee sex ratios: why do bumblebee colonies produce so many males?

Chair: Liselotte Sundström

14:10 Perttu SEPPÄ (Uppsala, Sweden)
Reproductive dominance in the social wasp Polistes carolina

14:30 Jürgen HEINZE (Erlangen, Germany)
Reproductive conflict in ant societies

14:50 Christian PEETERS (Paris, France)
Honest information, aggression and olfactory recognition of reproductive status in the queenless ant Dinoponera quadriceps

15:10 Elisabeth STERCK (Utrecht, The Netherlands)
Coinciding and conflicting sexual strategies shape the social organization of Thomas langurs

15:30 Elena KOTENKOVA (Moscow, Russia)
Conflict in house mice:comparative analysis of social behavior in two sympatric related species: house mouse (Mus musculus musculus) and mound building mouse (Mus spicilegus)

Chair: Madeleine Beekman

16:20 Katja HOGENDOORN (Adelaide, Australia)
Egg limitation: a phylogenetic constraint for the evolution of sociality in carpenter bees?

16:40 Peter THORÉN (Uppsala, Sweden)
Multiple mating and male parentage in the bumble bee Bombus hypnorum as revealed by microsatellites

17:00 Jes PEDERSEN (Aarhus, Denmark)
Kin structure is maintained in a seemingly unicolonial ant population having close to zero relatedness among nestmate workers

17:20 Peter NEUMANN (Berlin, Germany)
Drifting of workers and drones as an evolutionary factor in the honeybee Apis mellifera (L.)

17:40 Michael LACHMANN (Stanford, USA)
The computationally complete ant colony: a framework for the study of the functional organization of an ant colony

THURSDAY 28 AUGUST LECTURE ROOM 8+9

Symposium S7 Evolution of parasitic diseases
Organisers: Dieter Ebert (Basel, Switzerland), Minus van Baalen (Paris, France)

Chair: Minus van Baalen
9.35 Introduction (Ebert)
9:40 Bruce LEVIN (Atlanta, USA)
The population genetics of adaptive evolution in primarily clonal populations of parasites
10:10 Jacob KOELLA (Aarhus, Denmark)
Evolutionary aspects of the malaria life cycle

Chair: Dieter Ebert
11:10 Paul SCHMID-HEMPEL (Zürich, Switzerland)
Parasites in socially structured populations
11:40 Paula KOVER (Bloomington, USA)
Correlation between virulence and vertical transmission and its consequences on the evolution of a plant pathogen's virulence.
12:00 Oliver KALTZ (Orsay, France)
Local adaptation in the anther smut fungus Microbotryum violaceum and its host plant Silene latifolia
12:20 Minus VAN BAALEN (Paris, France)
The units of selection in 'viscous' host-parasite systems

Chair: Oliver Kaltz
14:10 Alex KRAAIJEVELD (Ascot, United Kingdom)
Costs of resistance against parasites: trade-off between encapsulation ability and competitive ability
14:30 Margaret MACKINNON (Edinburgh, United Kingdom)
Genetic relationships between virulence and transmissibility in malaria parasites.
14:50 Rob SLADE (Brisbane, Australia)
Genetic variation in CTL epitope and flanking regions in Epstein-Barr virus
15:10 Jouni TASKINEN (Zürich, Switzerland)
Evolution of virulence in two trematode parasites of a bivalve mollusc
15.30 -

Contributed Session C6 Predators and Parasites

Chair: Jacques van Alphen
16:20 Jeanette BOT (Aarhus, Denmark)
Host genetic diversity and parasites: variation in the relative size of the metapleural gland in Acromyrmex leaf-cutter ants
16:40 Bas PELS (Amsterdam, The Netherlands)
Dispersal and the evolution of predator virulence
17:00 Markus FRISCHKNECHT (Hinterkappelen, Switzerland)
Switching rules in ideal free distributions: differences in prey patches may have no influence on the distributions of predators using probabilistic switching rules
17:20 Vincent JANSEN (Ascot, United Kingdom)
How to exploit a patchily distributed resource
17:40 Gerard DRIESSEN (Leiden, The Netherlands)
A hard life is always too short; an evolutionary argument for time-limitation.

THURSDAY 28 AUGUST LECTURE ROOM 2+3

Symposium S14 Genetics of fitness-related traits in model organisms

Organisers: Armand Leroi (Ascot, United Kingdom), Linda Partridge (London, United Kingdom)

Chair: Armand Leroi
9.35 Introduction
9:40 Peter KEIGHTLEY (Edinburgh, United Kingdom)
Response to selection for body weight in inbred mice: involvement of major genes
10:10 Tracey CHAPMAN (London, United Kingdom)
Reproductive conflict in fruitflies

Chair: Armand Leroi
11:10 Michael TRAVISANO (Oxford, United Kingdom)
The specificity of adaptation in Escherichia coli
11:40 Paul TURNER (College Park, USA)
Sex and the evolution of intrahost competition in RNA viruses
12:00 Ryszard KORONA (Kraków, Poland)
Fitness decrease due to accumulation of point mutations in mismatch repair deficient strains of yeast Sacchoramyces cerevisiae
12:20 Jan KAMMENGA (Wageningen, The Netherlands)
C. elegans as a model for genetic mapping of life-history traits

Chair: Paul Ward
14:10 Esther DAVIES (Edinburgh, United Kingdom)
Polygenic mutation rates for fitness traits in nematodes
14:30 Armand LEROI (Ascot, United Kingdom)
Body size evolution and the genetics of growth in C. elegans.
14:50 Esther BETRAN (Cambridge, United Kingdom)
Antagonistic pleiotropic effect of inversion polymorphism on body size and early life-history traits in Drosophila buzzatii
15:10 Margarida MATOS (Lisboa, Portugal)
Testing general theories of senescence: evolution of G-matrices and mean values of life history traits during the adaptation to a novel environment
15:30 Ricardo AZEVEDO (London, United Kingdom)
Life history consequences of egg size in Drosophila melanogaster.

Chair: Michael Travisano
16:20 Wolf BLANCKENHORN (Zürich, Switzerland)
Adaptive phenotypic plasticity in growth rate in the yellow dung fly
16:40 Paul WARD (Zürich, Switzerland)
Sperm length is a sex-linked quantitative trait in the yellow dung fly Scathophaga stercoraria (L.)
17:00 Thomas GUILLEMAUD (Montpellier, France)
23 years of evolution of adaptive genes in the mosquito Culex pipiens: allele replacement and changing environment
17:20 Maurice SABELIS (Amsterdam, The Netherlands)
Genetic polymorphism in prey choice of a soil-inhabiting predatory mite
17:40 Izabela LESNA (Amsterdam, The Netherlands)
Prey choice and associated reproductive success of a soil-inhabiting predatory mite

Symposium S19 Evolution of Exon/Intron structures
Organisers: Erwin Schmidt (Mainz, Germany), Marie-Louise Cariou (Gif-sur-Yvette, France)

Chair: Erwin Schmidt
9.35 Introduction
9:40 Rüdiger CERFF (Braunschweig, Germany)
Intron patterns in ancient duplicated genes support the exon theory of genes
10:10 Mitiko GO (Chikusa-Ku, Japan)
Statistical correlation of protein module with intron position

Chair: Marie-Louise Cariou
11:10 Arlin STOLTZFUSS (Halifax, Canada)
Intron 'sliding' intron phase and the diversity of intron positions
11:40 Sylvia DEWILDE (Wilrijk, Belgium)
Invertebrate globin gene structure
12:00 Thomas HANKELN (Mainz, Germany)
Intron evolution in insect hemoglobin genes
12:20 Charles MATTHEWS (Dunedin, New Zealand)
Ancient and recent duplication events in Artemia provide a model for intron positional stability

Chair: Erwin Schmidt
14:10 Jean-Luc DA LAGE (Gif sur Yvette, France)
Evolution of introns in Drosophila amylase genes
14:30 Klaus WOLF (Aachen, Germany)
The mobile group II introns in the mitochondrial genome of the fission yeast Schizosaccharomyces pombe
14:50 Elisabeth HARING (Wien, Austria)
Splicing patterns of M- and O-type P elements
15:10 Anna HÄRLID (Lund, Sweden)
Early avian evolution: molecular dating of the divergence between paleognathous and neognathous birds.
15:30 Christina TORTI (Pavia, Italy)
Tephritid fruit flies contain full-lenght mariner elements.

Contributed Session C5 Trade-offs in Animals

Chair: Marcel Visser
16:20 Petri AHLROTH (Jyväskylä, Finland)
Are dispersal length and wing polymorphism adaptive characters in a waterstrider Aquarius najas (Heteroptera, Gerridae)?
16:40 Peter CRNOKRAK (Montréal, Canada)
The genetic basis of the trade-off between calling and wing morph in males of the wing dimorphic cricket, Gryllus firmus
17:00 Michelle VERHOOG (Leiden, The Netherlands)
The influence of genes for melanism on the activity of the flour moth, Ephestia kuehniella Zeller
17:20 Tapio MAPPES (Jyväskylä, Finland)
Negative phenotypic and genetic correlation between litter size and offspring quality: optimal prenatal effort in the bank vole
17:40 Jarle NORDEIDE (Bodö, Norway)
Delayed sexual maturity of three-spined sticklebacks (Gasterosteus aculeatus) after introduction of fish predators-phenotypic plasticity?

THURSDAY 28 AUGUST LECTURE ROOM 11

Symposium S22 Genetic drift in natural populations
Organisers: Armando Caballero (Vigo, Spain), Michael Whitlock (Tempe, USA)

Chair: Armando Caballero
9.35 Introduction (Caballero)
9:40 Brian CHARLESWORTH (Edinburgh, United Kingdom)
The effect of deleterious mutations on variation and evolution at linked loci
10:10 Spencer BARRETT (Toronto, Canada)
Evidence for genetic drift in plant populations

Chair: Mikkel Schierup
11:10 Michael WHITLOCK (Vancouver, Canada)
The effective size of metapopulations
11:40 Thomas KRAFT (Lund, Sweden)
Positive correlation between recombination rates and levels of genetic variation in natural populations of sea beet (Beta vulgaris subsp. maritima)
12:00 Armando CABALLERO (Vigo, Spain)
Effective size and polymorphism for populations under selection and linkage
12:20 Snaebjorn PALSSON (Uppsala, Sweden)
Associative overdominance and background selection

Chair: Michael Whitlock
14:10 Barbara GILES (Umea, Sweden)
Effective Drift!
14:30 Renaud VITALIS (Montpellier, France)
Population genetics of subdivided plant populations with a seed bank
14:50 Georg ARMBRUSTER (Leipzig, Germany)
Allozyme frequencies of the loci Aat and Idh suggest selection by habitat in the highly selfing landsnail Cochlicopa lubrica (O.F. Müller)
15:10 Jinliang WANG (Edinburgh, United Kingdom)
Effective size and F-statistics of a subdivided population in the finite island model
15:30 Philippe LENFANT (Perpignan, France)
Analysis of temporal variation in genetic structure between year classes in meditarranean littoral fish, Diplodus sargus

Chair: Georg Armbruster
16:20 Mikkel Heide SCHIERUP (Aarhus, Denmark)
The number of self-incompatibility alleles maintained in a finite, subdivided population
16:40 Thomas STÄDLER (Frankfurt am Main, Germany)
Population structure, null alleles, and gene silencing in a highly selfing polyploid freshwater snail
17:00 Sylvain GANDON (Paris, France)
Evolutionarily stable dispersal rate in a metapopulation with extinctions and recolonisations
17:20 Evelyne HEYER (Paris, France)
Impact of drift and demography on gene frequency changes in the Saguenay population of North East Quebec
17:40 Olivier HARDY (Brussels, Belgium)
Spatial autocorrelation analysis and the estimation of gene dispersal within a continuous population: investigation by numerical simulations

POSTER SESSION

WEDNESDAY 27 AUGUST 14.10-15.50

All sessions will start simultaneously with a chaired round of three-minute explanations by the presenter at the site of the posters.

Poster sessions 1-5: Room 2
Poster sessions 6-10: Room 3
Poster sessions 11-16: Foyer 3

P1 Mating system, sex-asex, inbreeding
P2 Reproductive isolation, hybridisation, speciation
P3 Behaviour, social structures
P4 Parasites/herbivores and plant/fungal hosts
P5 Parasites and animal hosts + theory

P6 Genetic conflict + symbiosis
P7 Plasticity, developmental instability + plant life history
P8 Animal and human life history
P9 Microsatellites: properties and applications
P10 Population differentiation on geographical scale

P11 Phylogeny of species
P12 Phylogeny and methodology
P13 Genetic structure in conservation biology context
P14 Drift and metapopulations + theory
P15 Adaptation to harsh and man-induced environments
P16 Early evolution, molecule evolution

Poster session P1 Mating system, sex-asex, inbreeding

Chair: Leo Beukeboom

Jon ÅGREN (Umea, Sweden)
Inbreeding depression and biotic interactions in the perennial herb Epilobium angustifolium
Bengt BENGTSSON (Lund, Sweden)
The strange correlation between polyploidy and asexual reproduction in plants
Robert BUTCHER (Dundee, United Kingdom)
Venturia canescens Gravenhorst: a model for the investigation of evolutionary selection of mating strategies under complimentary sex determination?
Robert BUTCHER (Dundee, United Kingdom)
Venturia canescens Gravenhorst: an old friend with a new tale of sex determination
Carmen CALLEJAS (Madrid, Spain)
Genetic variability and phylogenetic relationships among populations of two endemic Spanish species of barbus (Cyprinidae) inferred from RAPD-PCR analysis.
Alf CEPLITIS (Lund, Sweden)
Sexual reproduction and genetic variation in Allium vineale
James COOK (Ascot, United Kingdom)
Is asexuality reversible in Andricus gall wasps?
Ana CUNHA (Ascot, United Kingdom)
Parthenogenesis in Aphelenchus avenae: is an endosymbiont involved?
Mona-Anitta LOHILUOMA-RIIHIMAKI(Oulu, Finland)
Quantitative variation in selfing Arabidopsis thaliana (L.) Heynh. and outcrossing Arabis petraea L.
Joop OUBORG (Nijmegen, The Netherlands)
RAPD variability within and among uni- and bi-sexual populations of Stratiotes aloides, the watersoldier
Mariëlle RADEMAKER (Leiden, The Netherlands)
Effects of flower number on pollen transfer in three hermaphroditic species
Peter VAN BAARLEN (Wageningen, The Netherlands)
Muller's Ratchet, meiosis and generation of genetic variation in sexual and asexual Taraxacum
Ron VAN DER HULST (Amsterdam, The Netherlands)
AFLP-fingerprints identify clones in asexual dandelions (Taraxacum, Asteraceae).

Poster session P2 Reproductive isolation, hybridisation, speciation

Chair: Steph Menken

Pierre BOURSOT (Montpellier, France)
Non-random re-association of parental genomes in backcrosses between the two subspecies of mice M. m. domesticus and M. m. musculus.
Erika BUCHELI (Orsay, France)
Host races of the anther smut fungus Microbotryum violaceum are different species
Alexander BUGROV (Novosibirsk, Russia)
Evolution of the neo-y chromosome in bulgarian pamphagidae grasshoppers
Nikolai MUGUE (Moscow, Russia)
Signs of hybrid speciation on the Fundulus heteroclitus (Teleostei; Fundulidau) subspecies boundary.
Anders ÖDEEN (Uppsala, Sweden)
Reinforcement in yellow wagtail (Motacilla flava)
Franco SPIRITO (Roma, Italy)
High levels of meiotic nondisjunction and nonrandom segregation in a chromosomal hybrid zone in the house mouse
Christiane STÜRZBECHER (Mainz, Germany)
Coexisting Gammarus types: A study on seasonal demographic fluctuation and hybridization behaviour.
Ludwig TRIEST (Brussels, Belgium)

Are hybrids and introgressed hybrids dominating in mixed populations of Primula vulgaris x Primula elatior?

Ludwig TRIEST (Brussels, Belgium)

Hybridization is not a dominating process in the Salix alba - Salix fragilis complex (willows)

Sergey TSARIN (Sevastopol, Ukraine)

The significance of attributes of sexual dimorphism for reproductive isolation between species of the group Myctophum asperum (Myctophidae, Pisces)

Poster Session P3 Behaviour, social structures

Chair: Jürgen Heinze

Else FJERDINGSTAD (Lausanne, Switzerland)

Queen mating frequency and offspring paternity in Atta leafcutter ants

Daniel FRYNTA (Prague, Czech Republic)

Sperm dimensions in 20 mice taxa (Rodentia: Muridae): phylogeny and promiscuity?

Tatiana GOLUBEVA (Moscow, Russia)

Development of behavior in homeothermic animals: critical periods of sensory systems development and environmental factors *(no abstract available)*

Marianne IMHOF (Wien, Austria)

Multiple mating without regret? Evidence from female Drosophila melanogaster

Pavel MUNCLINGER (Prague, Czech Republic)

Rapid evolution of agonistic behaviour in mice: searching for the phylogenetic pattern within palaearctic genera Mus and Apodemus

Eric PETIT (Erlangen, Germany)

Genetic structure of nursing colonies of the noctule bat (Nyctalus noctula)

Michael SCHWARZ (Adelaide, Australia)

The central limit theorem and benefits to group living for an Australian allodapine bee, Exoneura bicolor

Michael SCHWARZ (Adelaide, Australia)

Phylogeny, social behaviour and discordant evolution in Australian allodapine bees

Goran SPONG (Uppsala, Sweden) Presenter: Mats BJÖRKLUND

The effect of social system on genetic structure in lions, Panthera leo

Martin THIEL (Walpole, USA)

Evolution of extended parental care in marine peracarid crustaceans

John ZAMMIT (Adelaide, Australia)

Intersexual benevolence among siblings: a sex ratio modifier in fig wasps

Poster Session P4 Parasites/herbivores and plant/fungal hosts

Chair: Dieter Ebert

Jan BRUIN (Amsterdam, The Netherlands)

Inter-plant communication and anti-herbivore defense

Alan GEMMILL (Edinburgh, United Kingdom)

Parasite host-range evolution: experimental analyses of host-specific adaptation and host-switching

Oliver KALTZ (Paris, France)

Life history modification of Silene latifolia (Caryophyllacea) parasited by the anther smut fungus Microbotryum violaceum

Ahmed KORAYEM (Cairo, Egypt)

Development of parasitic potency and reproduction of nematodes exposed to certain sub-lethal nematicide concentrations

Julia MALEEVA (Moscow, Russia)

mtDNA polymorphism as a marker of Phytophthora infestans (Mont.) de Bary populations reorganization on territory of Russia in the 1990's.

Stephanie PAPPERS (Nijmegen, The Netherlands)
    Molecular and morphological evidence for host race formation in Galerucella nymphaeae (Coleoptera: Chrysomelidae)
Erica TAUBE (Montpellier, France)
    Sloths as arboreal herbivores: population strategies of Bradypus and Choloepus.
Anne VAN DIEPENINGEN (Wageningen, The Netherlands)
    Intra- and interspecific transfer in Aspergillus species

Poster Session P5 Parasites and animal hosts + theory

Chair: Jacob Koella

Marion COOK (Gex, France)
    Influence of parasite life history on host clutch size
Paul HIGGS (Manchester, United Kingdom)
    Modelling coevolution in multispecies communities
Camilla LAURÉN-MÄÄTTÄ (Ascot, United Kingdom)
    How to cope with toxic cyanobacteria? Experiments with the water flea Daphnia pulex
Vera LAVROVA (Moscow, Russia)
    Evolution of the broad specialized bacteria. Klebsiella as the example
Leena LINDSTRÖM (Jyväskylä, Finland)
    Visibility and the effectiveness of signalling
Bregje WERTHEIM (Wageningen, The Netherlands)
    Why do drosophilid flies produce volatile aggregation pheromones when it guides parasitoids to their offspring?
Fayez ZAKI (Cairo, Egypt)
    Increasing rates of parasitism of the larval parasitoid Bracon brevicornis (Braconidae: Hymenoptera) by using kairomones and pheromones
Stepanka ZITKOVA (Praha, Czech Republic)
    Changes in mouse behaviour induced by Toxoplasma gondii don't show an adaptive character
Janine PIJLS (Leiden, The Netherlands)
    Interspecific host discrimination in insect parasitoids: a review

Poster Session P6 Genetic conflict + symbiosis

Chair: Austin Burt

Beatrice ALBERT (Paris, France)
    Evolution of the plant mitochondrial genome: model dynamics of duplication and deletion sequences
José CASTRO (Palma de Mallorca, Spain)
    Lack of cytonuclear disequilibria and evidence of natural selection in the evolution of mtDNA in two natural populations of Drosophila subobscura
Fons DEBETS (Wageningen, The Netherlands)
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Konstatin PYLKOV (Moscow, Russia)
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BRAKEFIELD P. Sun 24 Aug 8.30 Plenary P. BRAKEFIELD

Paul M. Brakefield (Leiden Univ.)

The evolution of morphological diversity: genes and the development of eyespots

To more fully understand the evolution of morphology it is necessary to study genetic variation, developmental mechanisms and functional aspects of the phenotype within particular patterns of diversity. Eyespot formation on the wings of Bicyclus butterflies provides such an opportunity. Eyespot patterns in butterflies are extremely diverse and can be subject to strong visual selection. Each eyespot consists of concentric rings of scale cells containing different colour pigments and which differentiate around a developmental 'organiser' or focus. The developmental process leading to spatial variation in scale cell fate across the adult wing in early pupae can be studied by experimental manipulation and the use of molecular markers. We have been investigating how genetic variation influences this developmental pathway and, in consequence, the phenotypic diversity in eyespots. Such information will lead to a better understanding of the potential for constraints or biasses in the paths taken by morphological evolution. Furthermore, the study of eyespots is relevant to exploring the evolutionary roles of genes of major phenotypic effect and of many genes, each with small effects.

Prediction of life histories and intrinsic mortality in evolutionary experiments

S.C. Stearns

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Quantitative predictions of the evolutionarily stable states of fitness components can be made when constraining relations are known. Experiments in Drosophila confirm the differences predicted in developmental time, body size, fecundity and intrinsic mortality when adult mortality rates are changed. Reducing extrinsic adult mortality rates produces decreases in intrinsic adult mortality rates leading to an evolutionary increase in lifespan. This is the first experimental confirmation of a central prediction of the evolutionary theory of aging. The interaction of extrinsic mortality rates with intrinsic constraining relations is sufficient to explain these results.

Facilitation and constraints in the evolution of mutualism ?

Marie-Charlotte ANSTETT

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Parasitism is the ancestral state of most mutualisms. What kinds of traits facilitate the transition from an antagonistic to a mutually beneficial interaction? The only well formalised and tested scenario for the origin of mutualism is based on the evolution of vertical transmission of parasites (from parents to offspring, Yamamura, 1996), which leads to reduced virulence and sometimes to the evolution of mutualism. However, this scenario can apply only to symbiotic mutualisms, and even these include examples in which vertical transmission does not occur. For these, formalised models are lacking.

What other kinds of traits facilitate the evolution of mutualism? Can we identify traits, maintained by selection on other functions, that independently in different lineages acquire the same novel function in a particular type of mutualism? If such "pre-adaptations" exist, what factors intervene to alter the selection pressures acting on them and shape them as new adaptations? How recurrent and predictable is the evolution of mutualism?

Small differences in traits already present at the origin of the mutualism may lead to differences in how the mutualism functions and how it evolves. "Constraint" is the flip side of "pre-adaptation." While constraints are usually envisaged to limit the range of evolutionary possibilities, constraints may also open evolutionary pathways that are otherwise not possible. For some mutualisms, evolutionary stability appears to be based on a coevolutionary equilibrium between trait values for the two mutualists. In other cases, however, the interaction appears to be stabilised by constraints imposed by preexisting traits of one species that the associated species cannot evolve to overcome.

These points will be developed using as examples the fig/ fig wasp pollination mutualism and protective ant/plant interactions.

Adaptation and Divergence During 10 000 Generations of Experimental Evolution of *E. coli*

Richard E. Lenski

Center for Microbial Ecology, Michigan State University, East Lansing, MI 48824, USA

Bacteria have many features that make them very useful for experimental studies of evolution. Among these are rapid generations, which allow one to observe evolution for many thousands of generations, and large populations, which provide a continual supply of genetic variation by mutation. Also, the ancestral type can be preserved indefinitely, so that one can directly compare ancestral and derived genotypes for any trait of interest. Using markers, one can even place the derived and ancestral genotypes in competition, allowing their relative fitness to be measured in the experimental environment.

Twelve populations of *E. coli* have been serially propagated in a glucose-limited medium for more than 10 000 generations. All of the populations were started from the same ancestral genotype. The grand mean fitness relative to the common ancestor has increased by ~50%. The replicate populations achieved almost identical gains in fitness, diverging from one another by only a few percent. All twelve populations also increased substantially in average cell size, although with somewhat more divergence than was seen for fitness. For both mean fitness and average cell size, the rate of change was much faster early in the experiment than later, indicating that they were approaching some limits. Also, both mean fitness and average size showed punctuated dynamics, with the punctuation caused by the successive sweeps of beneficial mutations through an evolving population.

We have also examined the dynamics of variation among clones within populations. The relative importance of different population-genetic forces that affect this variation changes over time. Early in the experiment, most of the variation was transient, whereas frequency-dependent selection becomes more important over time and actually maintains some stable polymorphisms. Interestingly, the actual rate of mutation increased dramatically in some, but not all, of the populations. Complementation tests show that the elevated mutation rates are due to mutations that disrupt DNA mismatch repair. Thus, important changes in the genetic system can evolve quite simply and rapidly, and these changes may have profound effects on all subsequent evolution.

The replicate populations also diverged substantially in their abilities to compete for limiting substrates other than glucose. The replicate populations typically show enhanced competitive abilities relative to their ancestor for alternative substrates that use the same mechanisms of transport into the cell as glucose. By contrast, the replicate populations are more heterogeneous in their abilities to use other substrates, such as maltose, that use alternative transport mechanisms. These results imply that glucose transport was a very important target of selection in the experimental environment.

To test the effects of initial genetic state on subsequent evolution, 36 new populations were further propagated in the same medium, except that maltose was substituted for glucose. A single clone from each of the twelve glucose-adapted populations was used to found three new populations, and there was a very wide range of initial fitness values. At the end of 1 000 generations in maltose, the derived populations had substantially converged, with only a few percent variation among them in fitness on maltose. Nonetheless, there was a small but significant effect of initial genotype on the final fitness value, which bore no simple relationship with the ancestral genotype's fitness. Evidently, certain populations achieved slightly better adaptive solutions to the maltose environment by virtue of differences in their initial genetic state, which arose by chance historical events.

In summary, simple experiments with bacteria show: (i) adaptation by natural selection; (ii) both transient and stable genetic polymorphisms; (iii) chance divergence of replicate populations; (iv) substantial changes from the ancestral state in competitiveness, morphology, physiology, and even the genetic system; (v) punctuated dynamics and stasis; and (vi) historical constraints on evolutionary outcomes.

Hox genes, homeosis and the evolution of segment identity

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In arthropods, vertebrates, and probably most other animals, transcription factors encoded by the Hox genes serve as molecular markers for the position of cells along the major body axis. Individual Hox genes are activated at different positions in the early embryo, establishing a pattern that is maintained throughout much of development. The differential expression of these genes causes cells that would otherwise be equivalent to adopt different developmental fates in different regions of the body.

The Hox genes were first defined by 'homeotic' mutations that transform structures in one part of the body into those characteristic of another - for example, the striking Antennapedia and Bithorax phenotypes of *Drosophila.* Similar transformations in natural populations were first catalogued by Bateson, in 1894. We now know that they arise both by mutation, and following injury, during regeneration.

As long ago as 1904, Lankester suggested that the phenomenon of homeosis "may have given rise to permanent structural changes characteristic of whole groups of Arthropoda", but he added "supposing the abnormality once established to be favoured by natural selection." However, most recent authors, have argued that homeotic transformations could not possibly contribute to natural evolution, because such "hopeless monsters" would never be selectively advantageous. I argue here that recent changes in our understanding of the role and regulation of Hox genes provide a way out of this dilemma. They enable us to understand how evolutionary changes in these "master regulators" can contribute to the gradual transformation of body plans.

Genetic analyses carried out in the 1970s and 80s by Lewis, Struhl and others showed that the Hox genes serve to define segment identity. This was interpreted to mean that Hox genes were ubiquitously and uniformly expressed in whole segments, under 'monolithic' regulation. It is now clear that the regulation of the Hox genes is more complex . Whether or not a given gene will be active in a particular segment is defined in the early embryo, by signals that make certain of the Hox gene regulatory domains "open for business". However, each of these regulatory domains has a complex modular structure. In later development, these modules are regulated independently in different cell types and stages of development, even within a single segment. Moreover, this detailed regulation is important for the specification of segment identities. A single Hox gene can specify the development of several different segment types, and our studies on the *Ultrabithorax* gene show that this is in large part dependent on the precise spatial and temporal regulation of the gene. Changing the pattern of *Ubx* regulation within segments can alter fine details of segment development.

With this perspective, it is easy to understand how gradual changes in the regulatory elements of Hox genes may contribute to the evolution of segment morphology. Summed over time, such changes may lead to differences in Hox gene function between species that are comparable to the effects of overt homeotic mutations - even though no such mutations need ever have been fixed.

To test whether such changes have occurred, we have initiated a survey of Hox gene structure and expression in diverse arthropods. Orthologues of all the *Drosophila* Hox genes can be identified in Crustacea and Myriapods, implying that the diversity of body plans in the mandibulate arthropods depends primarily on changes in the role and regulation of existing genes, and not on the origin of new Hox genes. We have compared the expression of these Hox genes in insects and in the branchiopod crustacean *Artemia*. In so far as the Hox genes provide reliable markers for homologous segments, these comparisons suggest a novel evolutionary relationship between body regions in insects and Crustacea.

The tempo and mode of speciation revisited

J. B. C. Jackson

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The fossil record provides the only direct, if imperfect, evidence of the timing and rate of evolutionary change and the origin of species. The theory of punctuated equilibrium proposed that most fossil species exhibit no net morphological change for millions of years between geologically instantaneous bursts of morphological change associated with the splitting of lineages by allopatric speciation. Unfortunately the theory spawned vastly more rhetoric than data, but the few taxonomically rigorous studies of well sampled fossil sequences over broad geographic areas do strongly support the punctuational pattern. In contrast, most examples of long term gradual change are restricted to single characters or to small geographic areas.

The apparent predominance of punctuation does not contradict conventional neodarwinian evolutionary mechanisms, but it does significantly constrain the range of probable scenarios for speciation and macroevolution. For example:

(1) Morphological differences between ancestral and descendant species are typically so small that it is difficult to reject random genetic change as the mechanism of speciation over intervals longer than a few thousand years and generations.

(2) Changes in life histories observed from larval shells, and using other morphological characters independent of those used to discriminate species, occur only at speciation. This implies that major transitions in modes of development are also highly punctuated.

(3) Timing of speciation and extinction is not random, but rather is concentrated in pulses associated with major environmental change.

(4) Macroevolutionary trends result from differential rates of speciation and extinction rather than evolution within species.

The major problem with all of these results is that they come from a variety of taxa with very different biologies. We need model systems that are equally amenable to a full range of both biological and paleobiological analysis.

PIERSMA T. Thu 28 Aug 8.30 Plenary T. PIERSMA

Micro-evolution of shorebird migration patterns

Theunis Piersma

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Shorebirds belonging to the Charadriiform families Charadriidae (plovers) and Scolopacidae (sandpipers), with their annual migratory movements, spin a web of connections around the globe. All migratory sandpiper species, and many migratory plovers, breed in the boreal and arctic regions of the northern hemisphere but spend the nonbreeding season further south. They commonly travel as far as the tropics, and sometimes as far as the subantarctic. Both families originated in the late Eocene or Oligocene, 30-40 million years ago, during a period with warm climates when the first grasses also appeared. This was long before, 10 million years ago, the first ice caps and tundra landscapes started to form. Nowadays, these climatic and landscape features influence the biology of shorebirds to a great extent. The evolution of the extant shorebird taxa, and their migratory movements, has taken place in a world with frequent climate changes and great variations in the position and extent of suitable breeding and nonbreeding habitats.

To illustrate the possible evolutionary interactions between climate and distribution of habitat on the one hand, and the biological characteristics, including migration pattern, of shorebirds on the other, I will delve deeply into the mysteries of the red knot (*Calidris canutus*), a long-distance migrating shorebird with, nowadays, a truely global distribution. Red knots have a circumpolar breeding distribution and are confined to barren high arctic tundra and polar desert. Except for these 6-8 weeks of polar summer, they live as fully marine birds in open coastal areas with suitable patches of feeding ground, radiating out of the arctic to different parts of the world. Red knots are mollusc specialists. They have a exquisite feeding apparatus to detect statically buried bivalves in soft sediments even without touching them, they live in large flocks that may help them to localize the best feeding areas, and they have a digestive apparatus geared to crushing and processing hard-shelled mollusc prey.

Their sensory specialization allows them to exploit habitats unavailable to other shorebirds, but also confines them to coastal areas encompassing extensive intertidal flats with suitable densities of shellfish on offer. This tale may have another twist. Red knots and the other high-arctic breeding shorebirds appear to have opted for lifes lived in habitats with low parasite pressure (tundras and seashores), necessitating relatively small investments in the immune system yet allowing for relatively high physical exertion (migratory flights, thermoststic costs in severe weather) without detrimental effects.

Present-day red knots comprise at least six geographically distinct populations, five of which have been awarded with subspecific status, and each of which has a unique set of features with respect to migration strategy (nonbreeding latitute, length of flyway, length of longest ecological barrier, navigational context) and the underlying annual cycle (endogenously steered timing and rates of moults and mass gains). In spite of this large variation of life-histories, all the genetic evidence that has been accumulated until now suggests that the radiation is of rather recent origin; that red knots went through a severe population bottleneck during or after the last glaciation (10-20,000 years ago). On the basis of paleoclimatic and geomorphological reconstructions it is possible to outline a geographic scenario for this recent radiation, starting with a breeding population either in the North Sea Basin or in Beringia. The probable recency of this global (re-)colonization, shows the great evolutionary versatility of the genetic systems enabling red knots to annually circumnavigate much of the globe with daunting precision.

ABSTRACTS OF POSTERS, SYMPOSIUM TALKS, CONTRIBUTED TALKS

alphabetically on presenting author

from AANEN to ZUK

Reproductive isolation in the genus *Hebeloma*.

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The genus *Hebeloma* (fungi, Basidiomycetes) forms ectomycorrhizas with many different tree species in a wide range of ecological communities. There exist many intercompatibility groups ('biological species') within the genus. Many of these biological species are very closely related, as appears from both molecular and morphological data.

In the traditional concept of allopatric formation of biological species reproductive isolation develops as a byproduct of divergence by separation. For fungi it has several times been suggested that it may be the other way 'round: divergence arises after the development of reproductive isolation, which can be oligogenic in Basidiomycetes. However, there must be a direct advantage of (and hence selection for) reproductive isolation, e.g. ecological specialisation.

To test this hypothesis we compare data on interfertility, phylogeny, ecology and geography for closely related species, that are partially reproductively isolated (incipient speciation?). Firstly, we have found 2 closely related groups that are almost completely reproductively isolated. One of the two groups comes from the Swiss Alps above 2000 meters and grows with *Salix retusa* and *Dryas octopetala*. The other group has been found in the Netherlands, growing with other *Salix* species and *Populus*. Within the groups there is complete interfertility, between the groups fertility is very limited, although one individual from the Alpine zone is interfertile with all members of both groups! Secondly, a case where partial interfertility occurs with substantial molecular divergence has been noted in a 'species', that does not show ecological differentiation. These phenomena will be discussed together with data on ecological specialisation, gene flow and divergence.

Environmental variation and life history interactions in a host-parasite relationship

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The complete life cycle of the microsporidian *Edhazardia aedis* normally occurs over two generations of its mosquito host *Aedes aegypti*. In female mosquitoes infected as larvae, *E. aedis* produces binucleate spores for vertical transmission to their offspring. These larvae die in association with the parasite's production of uninucleate spores. These spores are then released for horizontal transmission among larvae. Alternatively *E. aedis* can complete its life cycle within a single generation of its host. Horizontally infected larvae go on to horizontally transmit *E. aedis* to other larvae: binucleate spores germinate within the host and continue with development usually seen in the vertically infected generation.

We show with experimental data that these patterns of transmission emerge from an interaction of host and parasite life histories. This interaction is induced by the effects that environmental conditions have on life history traits of *Ae. aegypti* relative to those of *E. aedis*. Of central importance is the speed of larval mosquito growth and age at pupation. Repeated horizontal transmission is more likely to occur as larval growth slows. This gives *E. aedis* longer to complete its life cycle. However, in many cases mosquitoes do emerge after *E. aedis* germinates binucleate spores for uninucleate spore production. Thus, potential vertical transmission success is sacrificed without horizontal transmission being achieved.

This life history behaviour of *E. aedis* becomes easier to interpret when vertical transmission success is viewed in terms of a female mosquito's reproductive success. When larval growth slows, mosquitoes will generally emerge as smaller adults with lower fecundity and shorter longevity. As such, the life history traits of these mosquitoes make them less attractive for vertical transmission.

The interaction of host and parasite life histories appears as a result of adaptation by *E. aedis* to reduce variance in its transmission success when faced with interactions of environmental conditions with its host's life history traits.

Inbreeding depression and biotic interactions in the perennial herb *Epilobium angustifolium*

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The magnitude of inbreeding depression in plants has been found to vary among environments, and typically to be higher in the field than in the greenhouse. In this study, we tested the hypothesis that inbreeding depression is magnified by biotic interactions (competition and herbivory) in the perennial herb *Epilobium angustifolium* (Onagraceae). The performance (survival, growth, and flower production) of selfed and outcrossed offspring of 20 maternal plants was monitored in two greenhouse experiments lasting for four months. In the first experiment, plants were grown at three different densities (1, 2, and 4 plants per pot). In the second experiment, half of the plants were subject to experimental grazing after 10 weeks of growth (during early flowering). There was a significant effect of plant density on the magnitude of inbreeding depression for dry mass of aboveground parts at four months. At the highest density, inbreeding depression for dry mass was almost three times as high as at the lowest density (0.55 vs. 0.19). The proportion of plants producing flowers decreased with increasing density. Inbreeding depression for this fitness component was 0.18 for plants grown singly and 0.53 for plants grown at the highest density, but this difference was not statistically significant. Inbreeding depression for dry mass and for the proportion of plants producing flowers were not affected by the grazing treatment. Inbreeding depression for flower number of flowering plants was 0.17 in the control group and 0.28 in the artificially grazed group, but this difference was only marginally significant ($P = 0.10$). The results indicate that both competitive interactions and herbivory may magnify inbreeding depression in *E. angustifolium*, and that biotic interactions may at least partly explain why estimates of inbreeding depression obtained in the field are greater than those obtained in the relatively benign greenhouse environment.

Molecular evolution of the *Cecropin* multigene family in *Drosophila*: functional genes *vs* pseudogenes

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The *Cecropin* locus is a compact cluster of genes involved in the immune response in *Drosophila*. In *D. melanogaster* it consists of three functional *Cecropin* genes (A1, A2 and B) and two pseudogenes.

Levels of polymorphism and divergence in the *D. melanogaster* species subgroup have been estimated by sequencing a 4 kb region encompassing the *Cecropin* locus in a sample from a natural population of *D. melanogaster*, and also in its close relatives *D. simulans*, *D. mauritiana* and *D. sechellia*.

The interspecific comparison has revealed independent loss of function of the A2 gene in the latter three species. In our sample of alleles of *D. melanogaster* and in its closely related species both the TATA box and the initiation signal are conserved in the two previously described pseudogenes. In addition, they both present an open reading frame (59 and 62 codons long, respectively) starting at the same initiation codon and with the same putative intron/exon boundaries. The evolution of these duplicated gene copies will be discussed both on the light of their pattern of variation within and between species and of their transcription.

The molecular organization of the *Cecropin* cluster has additionally been studied in *D. subobscura*, a member of the *obscura* group of species. In *D. subobscura*, unlike in the *D. melanogaster* subgroup, the cluster is not compact but split in two different chromosomal locations. The evolution of this multigene family will be discussed based on the distribution of functional genes and putative pseudogenes in both the *obscura* and *melanogaster* groups.

Are dispersal length and wing polymorphism adaptive characters in a waterstrider *Aquarius najas* (Heteroptera, Gerridae)?

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We studied geographical differences and influence of river size in dispersal length, wing polymorphism and overwintering survival in a waterstrider *Aquarius najas*. The species is wingless in Northern Europe, while winged individuals occur frequently in Central and Southern Europe. This latitudinal difference has been suggested to be genetically controlled. We collected mature individuals from ten different populations and raised their offspring in "common garden" laboratory conditions. Half of these populations were from southern and half from central Finland. Daylength and temperature do influence wing development among other species of waterstriders, and thus we maintained a similar short daylength and warm conditions for all populations. These conditions should be favourable for wing development in general. The dispersal rates of cultivated offspring were observed in natural conditions. Individuals that had originated from small rivers were observed to disperse less than individuals that originated from large rivers. Among laboratory bred individuals several winged individuals appeared, and their proportion varied between populations. The relative frequency of winged individuals was highest in the southern populations. Thus, apart from phenotypic plasticity there seems to be some genetic control over the occurence of wings, and the latitudinal trend coincides with the direction in natural populations over a larger European scale. Overwinter survival in our laboratory conditions was highest among the wingless individuals. The survival cost may explain why the proportion of winged individuals was lower in the northern populations with more extreme overwintering conditions than in the southern ones.

Female choice for good genes - major benefits or minor costs?

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There is considerable disagreement whether gaining viability benefits to the offspring could be substantial enough to overcome the cost of female choosiness. A recent review by Pomiankowski and Møller (1995) suggested that the "lek paradox" might be resolved by large indirect benefits as indicated by highly heritable ornamental traits. However, the published data seems to be biased towards the high heritability estimates, and heritabilities of sexually selected traits do not allow us to interpret whether there are any viability benefits for the offspring. We have looked for the currently available studies that have estimated the magnitude of correlated responses in offspring survival or related traits against sexual selection in males. The data include 22 studies and 6 of them report very large indirect benefits (correlated responses >0.30) and another 5 studies report smaller but statistically significant effects. Half of the studies did not find any significant survival, performance or fertility effects. This is a very high proportion given that in general less than 10 % of ecological papers report non-significant results for their main hypothesis. Thus, recalling that publication biases favour the appearance of papers with significant results, it may be that in general the viability benefits to offspring are small. However, female choice may still be operating, if costs of choice are small. Indeed, in very many mating systems male-male competition alone guarantees that females mate with a better than average male. In other systems, condition-dependent ornaments with typically high variance between males allows females to choose between males with minor costs of comparison.

Evolution of the plant mitochondrial genome: Model of dynamics of duplication and deletion of sequences.

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The plant mitochondrial (mt) DNA is larger and more complex than its animal counterpart.The recombination between repeated sequences generate a set of molecules which comprise the plant mitochondrial genome. The molecules differ in size and vary in molecular structure. Different compositions of molecules have been observed within or between species. Although most genomes evolve principally by point mutations, the plant mt genome has a very low substitution rate, and its evolution is characterized by a lot of structural rearrangements.Changes in equilibrium of molecules can correspond to deletions and duplication of sequences. Several hypotheses have been postulated to explain the occurrence of deletion-duplication events when two sets of recombining repeats are involved. A model considering three levels of selection (molecular, mitochondrial and cellular) which simulates the dynamic of mitochondrial molecules has been built up to test these hypotheses. The model shows that whatever the recombination rates between repeats, if a mitochondrial sequence becomes unnecessary for the proper function of the mitochondrion, this sequence can be deleted and as a consequence another sequence will be duplicated. The organization of the sequences in relation to the origin of replication has a great influence over the dynamics of the deletion-duplication events of the plant mitochondrial genome. Effectively, depending on the sequences considered, the molecular level of selection will be in conflict with the mitochondrial and cellular levels. It appears that the presence of repeated sequences is very efficient to loss unnecessary mt sequences.

Implications of Molecular Genetic Species Concept (MGSC)

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The MGSC implies that organisms featured by specific genomic structure constitute a species. Experiments with bacteria, protozoans, yeasts and fungi resulted in finding that above 10% total amount of mutations found elsewhere in a genome separate one species from another. The corresponding data will be presented and discussed in details.

At a time the application of the UP-PCR to study high eukaryotes resulted in finding a comedown trend in total mutation rate from prokaryotes (bacteria) and simple eukaryotes (protozoans, yeasts/fungi) to high eukaryotes (plants and animals). This will be well illustrated in potato, wheat of plants and Cricetidae and primates of animals.

How does the trend uncovered relate to the MGSC?

ORDINARY VIEW
The MGSC is appropriate in most prokaryotes (bacteria) and simple eukaryotes (protozoans, yeasts/fungi) but has no sense in high eukaryotes which do not contain established (well separated from relatives) species because of low (negligible) mutation rate. Species complexes in bacteria and fungi which are revealed more and more now are also out of its application.

PROMISING VIEW
The MGSC fits well all known organisms disregarding their taxonomy (e.g., humans and apes are of one and the same species but they plus African green monkey are of one species complex) and provides general base for their classification.

Domestication of Wheat (*Triticum*) in the Middle East, evidence from High Molecular Weight Glutenin Subunit Genes.

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According to archaeobotanical evidence, wheat was domesticated in the Fertile Crescent of the Middle East about ten thousand years ago. The current hypothesis is that this event occurred only once, all of the cultivated wheats seen today deriving from this single origin.

The high-molecular-weight (HMW) glutenin subunits of wheat are coded by a multiallelic, multigene family. We have obtained partial allele sequences from a range of modern bread wheats, primitive cultivars, wild wheats and archaeological specimens, the latter studied by ancient DNA techniques. Phylogenetic analysis divides the allele sequences into a series of clades, one for each locus. The results enable the genomic constitutions of unidentified wheats to be assigned and permit us to allocate tentative timescales to the origins of the four principle genomes involved in wheat evolution, A, B, D and G. Sequences obtained from the B genome indicate the existence of two separate gene lineages which predate the time of domestication, possibly indicating that there were two independent domestication events.

Bacterial plasmids, horizontal gene transfer and biological evolution.

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Bacterial plasmids and other "satellite" genetic elements are easily transferred between bacteria, and from bacteria to eukaryotic cells; conjugation seems to be the most powerful mechanism of gene mobilization in and from prokaryotes. Plasmids often act as "collections" of other mobile genetic elements, such as transposons and integrons, and then as master inter-cellular mobilization vectors, mainly through conjugation. Broad-host-range conjugative plasmids are capable of being transferred to and expressed in very distantly related bacterial groups. Other common plasmid-mediated traits, such as adherence, also enhance gene transfer between neighboring microorganisms, and between bacteria and higher organisms to which they are associated. The increased ability of some pathogenic bacteria to survive within an infected host has been attributed to the acquisition of genetic determinants from the host. Also, the potential transfer of bacterial DNA sequences to mammalian cells has been documented. Along with the ability of plasmids to co-evolve and increase bacterial fitness, and to act as genetic "back-ups", these genetic elements have played a key role in bacterial evolution.

The presence of conjugative elements before the massive use of antibiotics allowed the fast emergence and spread of antibiotic resistance genes among clinically important bacteria. Antibiotic abuse may be acting as a selective pressure favoring more powerful transfer mechanisms and/or weaker restriction systems in recipient cells. However, since conjugation existed before the use of antimicrobial drugs, it is clear that other selective forces should favor the presence of these traits. By transforming recipient cells into donors, a two-step retrotransfer process enables the initial donor to also gain additional genetic information; this genetic exchange may be the selective advantage that conjugation provides to donor cells. It is important to ascertain the selective forces behind the prevalence of gene transfer traits, in order to better understand bacterial evolution, particularly in recently occurring phenomena, such as the emergence of antibiotic resistance.

Phylogenetic implications of novel homeobox sequences isolated from Myxozoan parasites.

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Phylum Myxozoa is a group of organisms whose biology and taxonomic placement are not well established. This phylum contains some 1200 described species, all obligate parasites, but the evolutionary relationship of the phylum to other major groups is obscure. Morphological characters, in particular the presence of polar capsules, structures which are extremely similar to cnidarian nematocysts, have suggested a close relationship to the Cnidaria. Recent analysis or 18S ribosomal sequences has given rise to competing hypotheses, one of which clusters the Myxozoa with bilateral animals, the other of which places the Myxozoa with the Cnidaria. We have employed molecular techniques to address these issues. Most recently we have used the polymerase chain reaction (PCR) to amplify homeobox sequences from several species of Myxozoa and their hosts. In the course of a preliminary survey, we have identified several novel homeobox sequences which we believe are myxozoan. Preliminary analysis of the sequences adduces similarities to classes of genes found in triploblasts, but which are absent in diploblasts. If borne out by further investigation, this would lend support to a phylogenetic hypothesis which places the Myxozoa with the Bilateria.

Mitochondrial plasmids in *Silene vulgaris*

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Plasmid like DNA-molecules have been found in the mitochondria of many higher plants, but our knowledge about their effects and genetics is still very limited. Most of the available information comes from cultivated species, such as maize, rape-seed, sugar beet and sorghum, whereas very few studies have been made on the occurrence and population dynamics of plasmids in natural populations. From rape-seed and wild beet we know that mt-plasmids can be inherited paternally, via pollen, which gives them a population dynamics different from that of mitochondria.

We have found mitochondrial plasmids in the bladder campion (*Silene vulgaris*), a gynodioecious member of the Caryophyllaceae family. To study the inheritance of these elements and what effects they may have on their carriers, crosses between plants with and without the plasmids have been performed. We have also tested 26 populations from southern Sweden for the presence of mt-plasmids. They were found in eight geographically well separated populations, with local population frequencies varying from a few to hundred per cent. The population differentiation with respect to the plasmids will be compared to the corresponding differentiation for nuclear and mitochondrial markers.

Strong selection might have favored every step in the transition from diploid asexuality to one and two-step meiosis.

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Kondrashov (1994) argued that the transition from asexual diploidy to the ploidy cycle was favored by a reduction in the genetic load. Antezana and Hudson (1997a) showed that the cycle can decelerate Muller's Ratchet and can lead to an increase in the number of nucleotide sites with optimal base occupancy (1997b). They also argued that, if the mutations of the genome are not recessive and are distributed more or less randomly over homologous chromosomes, a mutant undergoing the cycle can fix its least mutated chromosome(s) and thus increase its fitness drastically after a single generation (1997b). Here I present a strong advantage for replacing the step of the cycle in which one of the two haploid genomes is destroyed at random, with a cell division that results in two haploid cells. A mutant lineage that undergoes this segregation/multiplication step should have a higher growth rate than lineages that multiply only through mitotic events after the ploidy cycle; and should have as only disadvantage the halving of the cytoplasm of its cells of reduced ploidy. Adding syngamy between the reduced cells to this "segregative ploidy cycle" would lead to a primitive one-step meiosis. Rose (1983) pointed out that infectious genetic elements that cause cells to fuse might have driven the initial syngamy events in the history of eukaryotic sex. He also assumed that these events were deleterious. I argue, in contrast, that such syngamy events could have resulted in strong and even immediate fitness gains if the genome was subdivided into a moderate number of chromosomes. Under such conditions, indeed, inter-chromosomal recombination can expose to selection cryptic variance in fitness that can be created and maintained in non-recombining populations (Antezana and Hudson, 1997b). Thus, this cycle of segregation and element-driven syngamy and, through further fine-tuning, full blown one-step meiosis, might have been strongly favored to arise from the "segregative ploidy cycle". Finally, I argue that standard meiosis was favored to arise from one-step meiosis because it reinstated, without interfering with any population genetic advantages, the multiplication step that was lost when the syngamy step of one-step meiosis was established.

Population genetic studies of African bovids - implications for conservation

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Sequences of the mtDNA control region and microsatellite repeat number variation have been analyzed for a number of African bovid species throughout their range. The spectrum of results is illustrated with date from: Grant's gazelle, waterbuck, wildebeest, hartebeest, topi and African buffalo.

Generally we find unexpected high levels of genetic variation both within and among populations. The latter could often not be anticipated from morphological differentiation. The genetic variation is very differently structured within species from little differentiation to high levels similar to what is observed among morphologically easily distinguishable species.

All individuals have been sampled from extant populations and it is attempted to estimate to what degree the current population samples reflects the natural situation from before the impact of modern civilization. For all individual samples from four species microsatellite and control region data exist and the population differentiation of nuclear and mitochondrial variation is compared.

Selection on *t* haplotype chromosomes in natural populations of house mice (*Mus musculus domesticus*).

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t haplotypes remain one of the best described examples of non-Mendelian transmission (meiotic drive) in mammals. They are transmitted at high levels (≥95%) from heterozygous males, however, this powerful selective advantage is counterbalanced by both the complete sterility of *t*/*t* homozygous males, and the recessive lethal mutations carried by most *t* haplotypes. Numerous theoretical analyses have shown that the balance of these forces will result in a high frequency equilibrium of *t* haplotypes in natural populations (~75% +/*t* heterozygotes). Empirically observed frequencies are typically much lower than this, however (~15% to 25%), which has remained a paradox. Using molecular techniques to identify *t* haplotypes, coupled with ecological and genetic analyses of mouse populations, I have investigated the selective forces maintaining this polymorphism in natural populations. From a large population survey I found that the overall frequency of *t* haplotypes was even lower than most previous estimates, and that *t* haplotypes were patchily distributed and rare. To determine whether modifiers of drive might play a role in reducing *t* haplotype frequencies, Transmission Ratio Distortion (TRD) levels were measured in wild mice, but there was no evidence that TRD levels were lower in wild populations than measured in the laboratory. Several other factors that might contribute to the overall low frequency of *t* haplotypes were identified, however. These include the size and stability of populations, gene flow within and between populations, selection against +/*t* heterozygous mice, and multiple mating by females.

Allozyme frequencies of the loci Aat and Idh suggest selection by habitat in the highly selfing landsnail Cochlicopa lubrica (O.F.Müller)

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In central Europe, Cochlicopa lubrica is a widespread landsnail species. Its main breeding strategy is self-fertilization. Due to the high selfing rate, heterozygotes are extraordinarily rare and are therefore ommited in this study. At the loci Aat and Idh, two allelic strains were found to be most common: i) Aat AA / Idh BB, and ii) Aat BB / Idh AA. The other allelic combinations AA / AA and BB / BB were observed only occasionally with 32 and 8 specimens out of the 677 individuals.

For the Aat locus additional information is given. 29 central European populations were investigated with a total of 795 individuals. The phenotypes AA are significantly more frequent in dry and exposed habitats (road sites, field sites, grassy slopes, meadows) than in moist and shady habitats. The phenotypes BB occur preferably in moist and shady habitats (moist forests, river bank sites, bogs). These molecular differences between populations can be found even within a distance of only few hundred meters. It is suggested that selection by habitat is the main operating force for the arrangement of the AAT frequencies of the populations. Therefore, the rate of gene flow ($N_e m$) between the selfing populations is difficult to determine. Because of high selfing, a strong linkage of (preliminary) unknown loci is maintained. Selection can also operate on those linked loci.

The AA and BB types are morphologically very similar. With discriminant analyses of four shell dimensions, both selfing strains cannot be separated effectively.

Gene flow and natural selection in Louisiana irises

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Natural hybrid populations from crosses between species of Louisiana irises are common in areas of sympatry. Furthermore, the hybrid populations are characterized by the presence of mainly recombinant individuals with less frequent parental plants. Another common characteristic of the hybrid zones is that the adult hybrid plants possess genotypes that resemble one or the other parent. Few, if any, “intermediate” genotypes are found in the hybrid zones. In addition, no adult F_1 hybrid plants have ever been detected in surveys of hundreds of individuals from several hybrid zones. These results suggest that F_1 hybrids are rarely formed, but when formed result in a relatively higher frequency of hybrid formation. The F_1 generation may thus be both a bottleneck and catalyst in the formation of hybrid zones. We have examined various factors that may limit the formation of the F_1 generation between *Iris fulva* and *I. hexagona*; these include 1) pollinator preference, 2) gamete competition and 3) natural selection. We have also examined the frequency at which F_1 and later generation hybrids are formed in mixed populations of these two species. These data indicate that there are multiple, strong barriers to F_1 formation, but that once F_1 individuals become established gene flow and the evolution of hybrid zones are greatly enhanced.

Sensitivity of plant developmental rate to non-vernalizing temperature: a theoretical analysis stimulated by observations on cereals

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In addition to any effects of winter chilling, temperature affects the timing of flowering and of crop harvest. Even in places away from the hot drought-prone extremes of a crop's geographical distribution, plant development is accelerated faster than growth by warm summer temperatures so that plant size-at-maturity and cereal crop yields are reduced - by at least 4-10% for a 1°C rise. Genetic variation in sensitivity of developmental rate to temperature does exist, so breeding to reduce this shortfall in yield may be possible. But two major problems remain. First, almost nothing is known of the genetic control of developmental rate sensitivity to temperature. Second, the advantages of different degrees of sensitivity of developmental rate to temperature in particular environments are not known.

Here I use an adaptive theoretical framework to consider a variety of potential advantages of sensitivity of developmental rate to temperature in particular environments. From this I predict the adaptive pattern of developmental rate sensitivity in different environments during ontogeny and at different times of year, and compare these predictions against available evidence. The following hypotheses are examined: drought avoidance; developmental convergence on an optimal flowering date; unavoidable senescence or constraints on resource acquisition; selection for other traits that correlate with sensitivity of developmental rate to temperature. While drought avoidance may be the most obvious advantage of developmental rate sensitivity to temperature, evidence from a land race of barley suggests that other hypotheses should not be ignored.

Atkinson, D. & Porter, J.R. (1996). Temperature, plant development and crop yields. *Trends in Plant Science* **1** , 119-124.

The impact of special demographic behaviour in a human population on allelic and haplotype frequencies and its consequences on the estimation of demographic and genetic parameters

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We want to find out the most valid population genetic model for an expanding human population of Saguenay in Quebec. Since the demographic history of this population is well known and since we have some molecular data on the present day population, we are able to test the adequacy of our model. Demographic data include the distribution of effective offspring i.e. the number of married children per married woman which is rather similar to a geometric distribution and therefore differs strongly from the Poisson distributions which are usually used in simulations. We also know that these number of effective offspring are highly correlated between mothers and daughters (r2=0.95 for two generations in the 19th century). Molecular data are available on allelic frequencies as well as on the haplotypic frequencies for markers loci closely linked to disease genes which are common in this population. These genes are at very high frequencies (the carrier frequency is above 1/50) and in strong linkage desequilibria with surrounding microsatellite markers.
Our model is based on a branching process which allows to calculate, for a given distribution of effective offspring and a given between generation correlation, the distribution of the allelic and haplotype frequencies. We show that both the high variance of the distribution of offspring and the between generation correlation are needed to explain the high frequencies of disease genes and the linkage desequilibria with neutral markers. Not taking these demographic processes into account leads to a wrong estimation of population size and/or of mutation and recombination rates.

Conservation genetics: Molecular perspectives

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Molecular techniques permit direct genetic appraisals of populations and species in nature. They can be put to service in conservation biology by providing focused information on the natural histories, behaviors, and phylogenetic relationships of particular endangered species, or by providing comparative conservation-relevant information for suites of unrelated species, as for example in the description of regional phylogeographic hotspots. Examples of both classes of application for molecular markers will be presented.

Patterns of leaf trait variation and covariation in *Iris pumila* across a light gradient

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Knowing the extent and structure of heritable variation in traits that contribute directly to functional adjustment to particular environmental conditions is of principal importance for making predictions about their capacity to undergo adaptive evolution in heterogeneous environments. In this study we explored the pattern of interrelationships of several leaf traits in *Iris pumila* across a light gradient using individuals originating from an open and a shaded population. The following leaf traits were scored on each plant: leaf area, specific leaf area, stomatal density, total chlorophyll concentration and chlorophyll *a* to chlorophyll *b* ratio. The average phenotypic responses to light level significantly differed among alternative light regimes for all traits studied and their magnitudes changed in accordance to ecophysiological expectations for optimizing potential to intercept radiant energy under light-limited conditions. Genetic analyses detected significant additive genetic variation for almost all leaf traits at each light level in both populations, suggesting their evolutionary potential to evolve under natural selection. Phenotypic and genetic (family mean) correlations among different leaf traits were unstable both across the light gradient and between the populations. Associations between some traits attenuated or even shifted in direction with level of light. Consistently negative genetic correlations were detected only between total chlorophyll concentration and the proportion of chlorophyll *a* to chlorophyll *b*, implying that simultaneous evolution of these two traits toward their individual optima could be constrained, although they possess additive genetic variation available for selection to operate on it.

Life history consequences of egg size in *Drosophila melanogaster*

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We used a novel approach to study the effects of egg size on offspring fitness components in Drosophila melanogaster. Populations that differed genetically in egg size were crossed and the female offspring from these reciprocal crosses were examined for life history traits. These flies expressed effects of egg size, because they developed from eggs of different sizes as a result of maternal genetic effects, but displayed an equivalent range of nuclear genetic variation. The crosses used four independent pairs of outbred populations, that differed in the pattern of covariation between egg size and life history traits, so that the maternal genetic effects of egg size on offspring characters could be contrasted to the associations present among the parental populations. Egg size showed positive maternal genetic effects on embryonic viability and development rate, hatchling weight and feeding rate, and egg-larva and egg-adult development rate, but no consistent effects on larval competitive ability, adult weight or egg size in the offspring. Our method revealed a pattern of causality that could not be deduced from inter-population comparisons and, therefore, provides a good way of disentangling the causes and consequences of variation in egg size while controlling for zygotic genetic effects.

Exactly solved mutation-selection models and quantum chains

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We reconsider haploid mutation-selection (muse) models with many loci, two alleles per locus, and complete linkage (or, equivalently, sequence space models over a binary alphabet). They are important to investigate, e.g., the mutation load and the variability of populations as maintained by mutation-selection balance. The fitness functions that have been tackled so far include the quadratic and Gaussian optimum models from quantitative genetics; these functions have been combined with various mutation models.

We enlarge the spectrum of tractable fitness functions, and of the mathematical tools applicable, by establishing an exact equivalence between the muse model (with bidirectional mutation at every locus, and arbitrary fitness functions) and an Ising quantum chain (a model from statistical mechanics). In this picture, mutation corresponds to interaction of spins with a transversal field, with the mutation rate as a temperature-like parameter. The fitness of a configuration corresponds to the energy due to interaction of the spins within the chain. The highly elaborate methods from statistical mechanics allow us to find exact solutions for the quadratic optimum model in cases where only approximations were available previously. At the same time, we obtain solutions for 'Onsager's landscape', a fitness function which captures some essential features of molecular evolution, like neutrality and flat ridges.

Stochastic simulations for finite populations yield results very similar to the deterministic calculations if the infinite system. Implications for muse balance and limits to evolution are discussed, as is the important matter of scaling of fitness functions.

Parasite transmission and its consequences for sexual selection in sticklebacks.

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The acanthocephalan parasite *Pomphorhynchus laevis* is transmitted by the amphipod *Gammarus pulex* to its next host, fish. The parasite is clearly visible through the transparent cuticle of *G. pulex* as a conspicuous orange spot. Additionally, with the onset of infectivity of *P. laevis* to its next host, *G. pulex* shows a changed photoreaction; it becomes less photophobic. When given a choice, hungry stickleback fish, *Gasterosteus aculeatus*, ate more infected than uninfected *G. pulex.* Experimental manipulation of the colour effects of the parasite in its intermediate host showed that both behavioural and colour changes in the intermediate host promoted parasite transmission.

In a field population near Bern, 75% of the adult sticklebacks were infected with *P. laevis*. Infected males had a lower reproductive success than uninfected males. Infected males had smaller pectoral fins, while the number of parasites correlated with the green intensity of the iris of the eye. *P. laevis* did not seem to affect the intensity of red throat coloration which is one of the criteria of female mate choice in this population. Feeding experiments with laboratory-raised fish showed that the intermediate host of the parasite is an important source of male red breeding pigments.

Lab-raised full-sib groups which were fed with a standardized number of infected intermediate hosts varied in their susceptibility to this parasite suggesting heritable variation in resistance. Thus females get indirect benefits when choosing parasite-free mates.

Male sticklebacks oxygenate the embryos in the nest by producing a water flow with beats of their pectoral fins. Fanning efficiency may therefore depend on pectoral fin size. Experimental reduction of pectoral fin size while caring for a standard number of embryos in enclosures in the field, resulted in an enhanced beat frequency. Proportional embryo losses were not affected by the reduction in fin size as compared to those in control males. The costs of smaller fins were reflected in an increase in developmental time of the embryos. In addition to getting indirect benefits, females thus also get direct benefits when choosing parasite-free mates.

Satellite DNA in Dolichopoda cave crickets: phylogeny versus geographic variation

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Dolichopoda cave crickets are patchily distributed with about 30 species in the North Mediterranean area from the Pyrenees to Turkish Armenia. The highest species diversity is found in the insular and peninsular regions of Italy and Greece. Most Dolichopoda populations depend strictly on natural caves but some have also colonized cave like habitats or man-made hypogean habitats. As is true for the majority of cave organisms, a high degree of geographical isolation and strictly allopatric speciation processes can be assumed for Dolichopoda populations.

We analyzed the specific pDo500 satellite DNA family present in all Dolichopoda species analyzed sofar. About 100 repeats were isolated from individuals of 27 populations from 9 species. Interspecific comparisons of the pDo500 sequences indicate that the mode of evolution of this specific sequence family is basically gradual; nucleotide substitutions seem to occur with at an almost constant rate.

Numerous populations of D. geniculata and D. laetitiae inhabiting Central and Southern Italy are put together to the geniculata-laetitiae species complex as they cannot be discriminated accordingly by genetic markers such as allozyme variability. These populations result from at least more than one radiation. The noncoding pDo500 satellite DNA seems to be an appropriate marker to investigate the initial steps of genetic differentiation of geographically isolated populations in the geniculata-laetitiae species complex.

Phylogenetic relationships within the genus Acomys (Rodentia, Muridae, Murinae) : investigations using cytochrome b gene analysis

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The genus Acomys, also called "spiny mice", is widely spread over Africa and Middle-East, living in dry to arid zones. Acomys is found in rocky habitat, and in many cases rocky isolates.

The monophyly of the genus is generally admitted, but the relations between species is much debated and has been many times rearranged, and many species are synonyms. These uncertainities are mostly due to discrepancies in interpretations of morphological data, and no study using DNA sequences analysis has been published until now. The present work investigates inter-species relationships by analysing the evolution of the mitochondrial cytochrome b gene.

This gene provides a strong phylogenetic signal, as shown by high statistical support of the reconstruction obtained. This topology confirms the plesiomorphic position of A. spinosissimus and A. russatus, and evidences a wide clade with three groups : A. dimidiatus from Near East, Acomys sp. from West Africa, and A. cahirinus from Cairo clustering with A. aïrensis from Niger.

Moreover, cyt b sequences show a very high similarity between A. minous from Crete, A. nesiotes from Cyprus, and A. cahirinus from Cairo, which strongly suggests the possibility of a human introduction. The two insular species being considered up to now as endemic, this result comes as a surprise, and raises questions about their actual taxonomic position.

Evidence for genetic drift in plant populations

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Stochastic processes such as genetic drift, founder events and population bottlenecks have often been invoked to account for patterns of genetic variation within and among populations. Indeed some models of evolutionary diversification require the operation of stochastic forces for the evolution of adaptation and speciation. While the theoretical effects of random processes on neutral genetic variation are well understood, there are remarkably few empirical demonstrations of the influence of stochastic processes on inherited traits of adaptive significance in natural populations. This is, in part, because of the difficulty of disentangling the individual and joint effects of natural selection and genetic drift on patterns of trait variation.

The plant sexual polymorphism tristyly provides a valuable genetic system for investigating the role of stochastic forces in natural plant populations. Theoretical models indicate that when the intensity of drift is high owing to small population size, genetic constraints imposed by the inheritance of the polymorphism result in a diagnostic signature of style-morph frequency variation. The loss of style morphs from populations by drift is non-random resulting in the more frequent loss of the short-styled morph, and to a lesser extent the mid-styled morph. The long-styled morph is rarely lost from populations through random processes alone. These theoretical predictions can be tested by surveying natural populations of tristylous plants.

Investigations of natural populations of several unrelated tristylous taxa (*Eichhornia*, *Lythrum*, *Decodon*) with contrasting life-history traits have demonstrated that genetic drift and founder events play an important role in affecting population structure and patterns of genetic variation. In addition, evidence is presented indicating that stochastic processes can play a critical role in destabilising the outcrossed mating system of tristylous populations leading to the evolution of predominant self-fertilization. This process requiring the interaction of drift and selection bears some resemblance to parts of Wright's shifting balance theory of evolution. Small effective population sizes in many plant species may mean that genetic drift plays a more important role in influencing patterns of variation than is often appreciated.

Why do pied flycatchers have fewer parasites than great tits?

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The pied flycatcher and the great tit are ecologically similar and share the same ectoparasite species. However, when the abundance of ectoparasites in nests was compared for the same study sites and year, I found that nests of pied flycatchers contain only half as many ectoparasites as those of the great tit. A similar trend was found in other studies of the ectoparasites of the two species. A further search through the literature showed that pied flycatchers also have less blood parasites than great tits. Several hypotheses to explain these differences in the level of parasitism are put forward and discussed. There is little or no support for hypotheses based on differential exposure, nest site selection, or variation in resistance through sexual selection. On the other hand the data are consistent with hypotheses based on two behavioural strategies (small clutch size, use of insecticidal material in the nest) or on differential parasite virulence. Experimental studies are needed to distinguish conlusively between the possibilities.

BEEKMAN M. Thu 28 Aug S3 M. BEEKMAN

Bumblebee sex ratios: Why do bumblebee colonies produce so many males?

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Ever since the publication of the influential paper of Trivers & Hare on the evolution of social insects, sex ratios have been used to test their relatedness asymmetry hypothesis. Because of haplodiploidy, females are more related to their sisters than to their own (potential) offspring. Therefore these females are more likely to become workers and help their mother (the queen) instead of reproducing themselves. However the queen and her workers are in conflict over the investment ratio in sexuals. Since workers are 3 times more related to their sisters than to their brothers, they prefer a 3 : 1 investment ratio (♀:♂). Yet, the queen prefers a 1 : 1 ratio because she is equally related to both sexes.

Instead of female biased or equal investment, bumblebee sex ratios are extremely male biased. At first this seems in contradiction to the relatedness asymmetry hypothesis. However, large cost differences between queen and male production results in different sex ratios depending on the amount of resources available. If resources are not limited two different reproductive strategies can be distinguished. Which of these strategies will be followed depends on the timing of male production: if the queen starts the reproductive phase with male-production, workers will initiate egglaying and the colony produces a male biased sex ratio. If queens are produced first in the reproductive phase, workers refrain from egglaying and bias the investment ratio in favour of females.

In this paper we show that both cost differences and the effect of worker reproduction can explain numerical male biased sex ratios in bumblebees without violating Trivers & Hare's hypothesis.

An upper limit to the size of genomes

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During evolution the number of genes in the largest genomes have increased. Concomitantly there has been an increase in what the organisms can do. To ensure the fidelity of replication, more and more "repair" genes have also been added to the genomes. Can this increase in gene number go on forever?

To study such questions I introduce "Genetic Machines", a kind of Universal Turing Machines with which the relationship between **instructions** and **performance** can be explicitly analysed. The performance of a Genetic Machine is judged from 1) its interaction with the environment, 2) the time needed for its instructions to run, 3) the frequency with which it malfunctions, and 4) the error rate in the transmission of its instructions.

It will be shown that a "realistic" Genetic Machine does not improve forever with an increased number of instructions. Given the opportunity, it will instead evolve towards an optimal, limited genome size.

The strange correlation between polyploidy and asexual reproduction in plants

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The diploid form of the hoary cinquefoil, *Potentilla argentea*, has for long been regarded as a natural facultative apomict. This turns out to be incorrect; in two investigated Swedish populations we found a high degree of selfing, some outbreeding, but no apomixis. The hexaploid form of the species, which grows sympatrically and is morphologically very similar, was found to be apomictic but showing traces of sexuality.

These results strengthen the observed correlation between apomixis and ploidy level in higher plants: diploids produce seeds sexually while polyploids produce seeds either sexually or asexually. We consider different explanations for this correlation, and add to the discussion information from plants reproducing asexually via bulbills.

On the role of sex-differentiated gene flow for the genetic differentiation in metapopulations

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The partitioning of genetic variation within and between local breeding groups is of interest both for conservation genetics and for evolutionary scenarios such as shifting balance evolution and group selection. We used identity measures to derive the genetically effective rate of migration (m_e) in an island model for various cases of sex-differentiated contribution to gene flow. The joint effect of sex-biased migration and skewed reproductive sex ratios was investigated in the traditional island model and in the Whitlock-McCauley model for transient local populations. In the island model, genetic differentiation between local populations may often be affected by the sex of dispersing organisms, as well as the timing of dispersal (before or after fertilization), especially so in the case of X-linked genes. In the Whitlock-McCauley model, when colonizers constitute a random sample from the metapopulation the effect of sex-biased migration may often diminish as extinction rate increases. On the other hand, when the founders of a population tend to originate from a single source, sex-biased migration remains potentially important even for high extinction rates. The degree of correspondence between the sexual bias in migration and colonization also has bearings on the model's predictions. For example, when migration is sexually biased such as that $m_e < m$, but colonization is much less biased, the condition for decreased genetic differentiation upon extinction may be relaxed. This means that extinction-recolonization events may more easily lead to decreased differentiation than what was originally predicted.

Antagonistic pleiotropic effect of inversion polymorphism on body size and early life-history traits in *Drosophila buzzatii.*

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In the cactophilic species Drosophila buzzatii there is evidence that second-chromosome polymorphic inversions have a biometrical effect on size-related traits. Because it has been reported that body size trade-off with larval developmental time in Drosophila, we study here whether or not those geneticmarkers have also an effect on early fitness components. In particular, we expect that polymorphic inversions make a statistically significant contribution to the genetic correlation between body size (as measured by thorax length), and larval developmental time. This contribution is expected to be in the direction predicted by the trade-off, namely, those flies whose karyotypescause them to be genetically larger should also have a longer developmental time than flieswith other karyotypes. From the results of two different experimental approaches, we conclude that there is a statistically significant contribution of the second-chromosome arrangements to the phenotypic variances of body size and developmental time in *D. buzzatii.* we also conclude that these arrangements make a positive contribution to the total genetic correlation between both traits, as expected by the suggested trade-off. The data do not provide evidence to wether the genetic correlation is due to antagonistic pleiotropic gene action, or to gametic disequilibrium of linked genes that have a biometrical effect on one or both traits. The results do suggest, however, a possible explanation for the maintenance of inversion polymorphism in this species, and provide the relevant genetic information to look for an overdominant locus that could be eventually mapped if it exists.

Validation of the sex locus concept in the honeybee using molecular data

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Sex determination mechanisms seem to be highly variable among the animal kingdom. In most sex determining mechanisms sex chromosomes are involved although the underlying genetic system may vary (e.g. genbalance or dominant sex determining factor). Some of these model systems are well studied even at the molecular genetic level.

In the honeybee (*Apis mellifera*) as in most Hymenoptera a total different mechanism of sex determination has been evolved. There sex is determined by one single locus with multiple alleles (Whiting scheme, Whiting 1943). According to this model eggs which are heterozygous at the sex locus develop into females while hemizygous and unfertilized eggs develop into males. Diploid males occur if the sex locus is homozygous.

Two markers were independently identified so far (Beye et al. 1994, Hunt and Page 1994), which were closely linked to the sex determining locus. The first results showed that both markers are linked to the same locus (Page and Beye, in prep) which favours the single locus concept (sex locus). Furthermore the sex locus was mapped onto chromosome 8 of the honeybee. These mapping procedures may provide a first tool in order to identify the sex locus gene.

A molecular model of the sex locus function is presented. e.g. bHLH transcription factors meet the requirements needed for a sex locus model which are also involved in the primary signal of *Drosophila* sex determination.

The study of this alternative mode of sex determination may give a new insight of evolution of sex determination mechanisms even outside the Hymenoptera.

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Hunt, GJ, Page, RE (1994) Molec Gen Genet 244: 512
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Host predisposition: effects of fungal infection of *Silene alba* on oviposition and performance of the noctuid *Hadena bicruris*.

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Herbivores and pathogens that share a common host species can affect each other's performance not only directly (e.g. through a vector relationship), but also indirectly, through alteration of the apparency or suitability of the host plant. Such interactions are likely to have implications for the evolution of plant defense. A case study is presented of pathogen-induced alterations of a host phenotype that are expected to reduce herbivore performance. We test whether a behavioural response by the herbivore (preferential acceptance of uninfected host phenotypes for oviposition) can be observed. Such a response may in turn reduce the relative fitness of uninfected, pathogen-resistant plants, and slow down the evolution of pathogen resistance in the presence of the herbivore.

Host plant in the model system is *Silene alba* (Caryophyllaceae), one of the hosts of the systemic, host sterilizing anther-smut fungus *Microbotryum violaceum* (*Ustilago violacea*). The fungus produces its spores in the anthers of infected flowers, in which pollen production is prevented and development of the ovary is halted, so that ovules do not develop into seeds. *Hadena bicruris* (Noctuidae), is an oligophagous nocturnal moth that is (i) pollinator, (ii) vector of fungal spores, and (iii) seed predator of *S. alba*. Nectar consumption and pollination obligately preceed oviposition on the ovary. Since infected plants do not produce the main food source of the caterpillars (seeds), we ask: (1) Is the performance of herbivore offspring oviposited on infected plants lower than on healthy hosts ? (2) Is the oviposition rate lower on infected than on uninfected plants ? (3) Does the strength of oviposition preference depend on the frequency of infected hosts ?

Environmental stress, detrimental alleles and the extinction probability of small populations

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Many populations of endangered species have to cope with an increase in homozygosity due to genetic drift and/or inbreeding in small populations. This may result in genetic stress often accompanied by inbreeding depression. Inbreeding depression has been a topic of interest from a number of perspectives, particularly in the conservation biology of endangered species. It is often argued that inbreeding depression in mainly caused by mildly deleterious mutations, because detrimentals with a large effect, such as lethals and sublethals, will be quickly purged from a small population. However, many detrimentals are expressed only under certain harsh environmental conditions, but may be nearly neutral under more benign conditions. In this paper I will explore the probability of fixation for such "conditional" detrimentals and discuss the possible consequences for the extinction probability of small populations.

Shallow geographic structure in the greenfinch Carduelis chloris as revealed by microsatellites

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Most species exhibit some degree of geographic structure with limited gene flow between distant populations and more extensive gene flow between adjacent populations. Consequently, adjacent populations are more similar genetically than more distant populations. A problem arises when very little genetic variation is found, which can indicate at least four things: extensive gene flow between areas, recent selective sweeps, recent bottlenecks or wrong genetic marker.

Recently, using both allozymes and mtDNA, we have shown that the greenfinch *Carduelis chloris* exhibit exceptionally low levels of genetic variation, and a very shallow, but clear, geographic structure. Based on this we concluded that this species has undergone a recent bottleneck which to a large extent removed genetic variation. However, since the genetic variation was so low few details could be obtained. Therefore, we analysed part of the data set by means of four microsatellite markers. As expected, these loci were far more variable, but the main conclusions concerning the geographic structure and gene flow remained. Furthermore, peculiarities in allele distributions within loci are consistent with the bottleneck hypothesis. Thus, these three molecular systems provide independent and congruent information about the demographic history of this species.

Adaptive phenotypic plasticity in growth rate in the yellow dung fly

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Two important factors that constrain growth and development are seasonality and food limitation. Both essentially are time constraints in non-dispersing organisms which deplete their habitat.

Full-sib families of yellow dung flies were allowed to develop under predator-free field conditions by varying the time before the onset of winter and splitting each brood into three environments differing in the amount of dung a set number of larvae had as a resource. At overabundant resources individuals maintained large body sizes, an adaptive response, by increasing their growth rate as effective development periods became shorter towards the end of the season, but when larval resources were limited by competition growth rates could not be increased. This was only apparent when the effects of temperature were removed by expressing development time in degree-days above a lower growth threshold. Overall, individuals showed slower growth, shorter development times (age at reproduction) and smaller adult body sizes (size at reproduction) when resources were limited. This disagrees with predictions of most life-history models, which typically assume proportionality of development time and body size while growth rate is always maximised. Elevated larval mortality in my experiment indicates physiological costs of fast growth independent of predation.

Growth rate (as well as body size, development time and diapause induction) was heritable but also showed significant heritable variation in phenotypic plasticity (genotype by larval environment interaction). This is possibly maintained by unpredictable spatio-temporal variation in dung abundance, competition and hence selection. With an analogous laboratory split-brood experiment I am currently testing the complementary prediction that heritable variation in phenotypic plasticity in growth in response to variation in the onset of winter should, in contrast, be low (i.e. non-significant) due to the comparatively high predictability of the onset of winter.

IS elements and genetic diversity during 10,000 generations of experimental evolution with *Escherichia coli.*

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Transposable elements (TE) promote the highest contribution to spontaneous mutagenesis in *E. coli* but their role on the genetic structure of bacterial populations has not been systematically evaluated. We have used the collection of 12 *E.coli* lines cultured for 10,000 generations by the group of R Lenski at Michigan State University to monitor the distribution of insertion sequences (IS) on the chromosome of *E.coli* B. During glucose-limited cultures, fitness increased in the 12 lines by 40% after 2,000 generations and 55% after 10,000. Locations of IS elements are made by RFLP using internal sequences as probes and reveal not only transposition of the elements but also other chromosomal rearrangements. We document several increases of genetic diversity in the cultures followed by drastic decreases due to periodic selection, and this defines families of individuals sharing a number of new IS-containing fragments. Similar processes are observed in the different independant lines, suggesting general mechanisms underlying the evolution of these bacteria.

The major fitness increament is before the first 2,000 generations and it is correlated to the renewal of the genetic structure. Some new IS insertions become predominent in the populations and this questions the role of IS elements for promoting beneficial mutations, for instance by controling expression of adjacent genes from their internal promoters. These new insertions are in the process of being sequenced to identify the nature of the mutations, and the biochemical functions allowing the improvement of fitness during 10,000 generations of experimental evolution.

The cnidarian premises of metazoan evolution: from triploblasty, to coelom formation, to metamery.

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The hydromedusan subumbrellar muscle tissues originate from a mass of ectoderm derived cells (entocodon) proliferating inwardly and separated by the ecto- and endoderm through a layer of extracellular matrix, thus forming a triploblastic organisation. By cavitation and differentiation, the entocodon gives rise to the striated and smooth muscle layers of the subumbrella. This suggests that not all Cnidaria are diploblastic and that the subumbrellar cavity is a coelom-like structure formed late in ontogeny, whereas the coelom in higher animals is normally formed during embryonic development. This view of cnidarian structures can be pushed further while considering the regulation of modularity and metamery. The occurrence of homeotic genes in cnidarians and other "lower" animals shows that the specification of body architecture has a common molecular ground throughout the animal kingdom. It is suggested that the expression of homeotic genes while specifying a given architecture might be regulated by iteration of their activity, leading to "low" modular organisms and to "higher" metameric ones. Replicated parts as modules and metameres might be analogous, but the affinity in their molecular specification (and possibly regulation) might indicate homology. The number of resemblances between cnidarians and "higher" metazoa suggests that this phylum might be a centre of metazoan radiation, having structures which represent the living premises of the main steps of animal evolution.

The evolution of sex-determining mechanisms in Diptera

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Among dipterans, different strategies are employed to select and stably maintain male or female development. Nevertheless, these strategies may be based on a common principle in which a primary signal controls the activity of a binary switch gene (1). In the best studied system, *Drosophila melanogaster*, the *Sxl* gene assumes this switch function. When ON, it imposes female development; when OFF, male development ensues. Likewise, genetic studies in the housefly, *Musca domestica,* have identified a putative master switch gene *F* which directs female development when ON, and male development when OFF (2).

We are taking two complementary approaches to address the question to what extent sex determination in *Musca* and *Drosophila* is based on conserved molecular mechanisms. On the one hand, *Musca* homologues of the known sex-determining genes in *Drosophila* (*Sxl*, *tra* and *dsx*) are being isolated and analysed for functional conservation. On the other hand, we are trying to directly isolate the genetically identified sex-determining genes, *F* and *M*, of *Musca*. The results of these efforts and their implications on our current view of how sex-determining mechanisms have evolved will be discussed.

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Selection at multiple loci: unifying selectionist's and neutralist's views of evolution

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The roles of drift and selection in evolutionary dynamics of multi-loci models have been investigated. For the haploid case it could be shown analytically that the selection coefficient for any given allele vanishes as the number of loci with selectively relevant alleles in the population increases. Hence, functionally distinct alleles that contribute differentially to an organism's fitness appear as if they were neutral or nearly so, given a large number of loci with selectively relevant alleles in the population.

Using an individual based model these results were corroborated and extended to the diploid case. This model was also used to test the influence of the underlying fitness model on these results. Additive, multiplicative, and mixed models were tested. In each model, drift was found to govern the dynamics when the number of loci with selectively relevant alleles was high, whereas at low numbers selection was found to drive the dynamics.

This model shows that a limit exists to average heterozygosity. In large genomes a high proportion of alleles will be purged out of the population randomly until selective forces in heterogeneous environments can stabilize polymorphisms. As a consequence, chances for selection at specific loci are limited because there will always be some chance involved in "nature's choice" of which loci are under selection.

It can be concluded from this model that the neutralist's and selectionist's views of evolution are possibly not mutually exclusive but rather two ends of the continuous spectrum of evolutionary dynamics of organisms with large genomes.

Host genetic diversity and parasites: variation in the relative size of the metapleural gland in *Acromyrmex* leaf-cutter ants

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Different defence traits against parasites may be optimised in different genetic lineages of workers in social insects. A higher genetic diversity among workers within colonies has been hypothesised to be beneficial for colony defence against parasites, because it will lead to the presence of more different genetic lineages. This may result in a better distribution of defence traits. The metapleural gland is one of the traits, which have been considered important for the defence of ant workers against pathogens, because it has previously been shown to produce substances with antibiotic properties. Other studies indicate that this gland is relatively large in those morphological castes of workers that are expected to need large quantities of antibiotic substances, according to the task they fulfil within the colony. The metapleural gland is considered very important in leaf-cutter ants, because these ants do not only have to protect themselves against pathogens, but their fungus gardens as well.

We have analysed the allometric growth of the metapleural gland in two species of leaf-cutter ants, *Acromyrmex octospinosus* and *Acromyrmex echinatior*. We also investigated the phenotypic and genetic background of size differences in the metapleural gland in major workers of *A. octospinosus* , by comparing the relative size of this gland for workers of the same colonies under field and laboratory conditions and for workers originating from different patrilines within colonies. For this species patrilines could be distinguished by using two allozyme loci and one microsatellite locus.

For the minor workers the increase of gland size with pronotum width was about isometric, but the slope of this relationship gradually decreased through the media to have a slope of around 0.45 for the major workers of both species of leaf-cutter ants. The genetic diversity between workers within colonies of *A. octospinosus* was found to be high, due to multiple queen-mating and occasionally also due to functional polygyny. Relative metapleural gland size increased significantly under laboratory conditions in three out of four colonies. Significant genetic variation for relative metapleural gland size and genotype-by-environment interactions occur in part of the colonies, indicating that a higher genetic diversity within colonies may indeed lead to a more optimal distribution of the gland size within the worker force.

Molecular analysis of "viviparous" and "ovoviviparous" populations of *Salamandra salamandra* in Spain.

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The urodele *Salamandra salamandra* show different reproductive patterns in the North of Iberian peninsula. Populations are known to give birth to just a few fully metamorphosed offspring in a derived mode of reproduction ("viviparity") contrasting with the species characteristic ovoviviparous reproductive mode.

In this communication, we present the analysis by RFLPs of mitochondrial DNA from 13 populations along a transect across the North of Spain exhibiting viviparous or ovoviparous reproductive pattern as complement to previous work from our lab (M.Alcobendas, H.Dopazo and P.Alberch. 1996. J.Evol.Biol. 9 83-102).

Phenetic and cladistic analysis of mitochondrial DNA divergence between the populations surveyed groups the isofemale lineages in two main clusters: One grouping mtDNAs from populations located at each ends of the transect, the other grouping populations from the central region. The last one shows higher diversification both in number of distinct haplotypes and overall genetic divergence and groups the most of the viviparous populations. Two others populations exhibiting optional viviparity have mtDNAS belonging to the first cluster.

A combination of allozyme and mtDNA data presented here allows to understand the dynamics of the isofemale lineages among the two reproductive modes and suggest that specific transition from ovoviviparism to viviparism could have arisen in *Salamandra salamandra* prior to the mitochondrial DNA differentiation.

The overall outcome emerging from molecular evidence outlines a unique model (*Salamandra salamandra)* where macroevolutionary events (acquisition of independence from the aquatic media) are amenable to analysis from a microevolutionary perspective.

Molecular phylogenies in the isopod-*Wolbachia* endosymbiosis

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Wolbachia are strictly endocellular, cytoplasmically inherited bacteria responsible for a number of reproductive disorders in arthropods. They are known to induce cytoplasmic incompatibility (CI) or parthenogenesis in insects and feminization, symptom only known in crustaceans. All these effects enhance their own spread in the host populations. According to a large survey from different authors, *Wolbachia* is widespread in insects, occuring in 10 to 20% of species. In crustaceans only a few species are known to be infected.
By using diagnostic PCR primers we have found *Wolbachia* in about twenty isopod species: *Wolbachia* is widespread in Oniscidea (terrestrial isopods) occuring in all families of this clade and is also present in Asellota and Flabellifera, two different suborders of Isopoda group. The taxonomic status of these microorganisms has been defined by sequencing parts of their 16S rDNA and ftsZ genes. All these crustacean symbionts belong to the B subdivision of *Wolbachia* . The bacteria from Oniscidea hosts show a very low divergence and form a monophyletic group. Bacteria from Asellota and Flabellifera are more close to parthenogenesis and CI *Wolbachia* of insects.
Phylogeny of the hosts has been determined with nucleotide sequences of their large subunit (lsu-rRNA) of mitochondrial ribosomal gene. The sequences show a high degree of variability and isopods are more diversified than previously expected. In particular, the Oniscidea group seems to be paraphyletic. Since the single clade of *Wolbachia* from oniscideans imply a single original infection in a common ancestor of the included hosts, the lack of concordance between bacterial and host phylogenies indicates that the crustacean-infecting *Wolbachia* have undergone horizontal transfer amongst closely related oniscidean lineages. The position of the bacteria from Asellota and Flabellifera indicate that *Wolbachia* lineages have sometimes been transmitted between insects and crustaceans.

Non-random re-association of parental genomes in backcrosses between the two subspecies of mice *M. m. domesticus* and *M. m. musculus*.

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The two subspecies of house mouse *Mus musculus domesticus* and *M. m. musculus* have evolved partial genetic incompatibility, as judged from the patterns of limited and differential introgression in their natural hybrid zone, and the existence of partial or total sterility of hybrid males. In order to better understand the interactions between the two genomes, we analysed the backcross 1 (BC1) progeny between several wild-derived stocks belonging to the two subspecies. The segregation of alleles at 35 microsatellite loci distributed in the genome was studied. Deviations from Mendelian transmission were never systematic at any locus, but were detected in certain combinations of the different factors considered in the analysis (strains used in the cross, direction of the backcross and sex of the BC progeny). Multilocus associations appeared different from those expected by chance, when tested by comparing the distribution of heterozygosity in the BC to that obtained by simulations and resampling. In a cross involving fully inbred strains, an excess of recombined gametes was transmitted by the F1 females. However, in a cross involving random bred parental strains, an excess of parental multilocus combinations was found, suggesting either counter-selection of recombined genotypes or some form of chromosomal affinity. A positive correlation was observed between the fertility of F1 females and the heterozygosity of their BC progeny. Negative interference was found on the X chromosome, suggesting a disruption of the normal meiotic process on this chromosome. Overall, the data suggest deviations from normal meiotic segregation and recombination in the F1 females. Selection on the multilocus genotypes of the BC could also participate in creating the patterns observed. Ways of distinguishing the two phenomena will be discussed.

Chaperonine Hsp60 and Hsp70 encoding genes in anaerobic chytrids.

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Anaerobic fungi are inhabitants of the digestive tract of many herbivores, where they play an important role in the digestion of plant material. The anaerobic fungi lack mitochondria, but contain an organelle called the hydrogenosome. The evolutionary origin of the hydrogenosomes is an unsolved question. An endosymbiotic, a cytoplasmic and a mitochondrial origin have been postulated. Ultrastructurally, the hydrogenosomes of anaerobic fungi strongly resemble peroxisomes. Furthermore, the genes encoding the hydrogenosomal adenylate kinase of *Neocallimastix* sp. *L2* and *Piromyces* sp. *E2* have been isolated. Analysis revealed the presence of a peroxisomal targeting signal, the tripeptide SKL. However, phylogenetic analysis of these genes revealed that they are closely related to orthologous genes encoding mitochondrial adenylate kinases. Therefore, a chimeric origin of the hydrogenosomes is likely.

In order to study whether a mitochondrial import system is still present, we isolated genes encoding for the chaperonines Hsp60 and Hsp70 of the anaerobic fungi *Neocallimastix* sp. *L2* and *Piromyces* sp. *E2*. In eukaryotes, Hsp60 is localized in mitochondria and chloroplasts. Hsp70 is localized in the cytosol, in the endoplasmatic reticulum, in mitochondria and in chloroplasts. Phylogenetic analysis of the Hsp60 and Hsp70 genes will reveal whether mitochondrial Hsp60 and Hsp70 genes are present in anaerobic chytrids.

Effects of Wolbachia symbionts on reproductive isolation and fitness of their spider mite host (Tetranychus urticae)

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Knowledge of the genetic basis of reproductive isolation is important for understanding speciation. Most empirical and theoretical studies on reproductive isolation have focused on the role of nuclear genes. However, the fact that an important fraction of the heritable material of an organism is non-nuclear (cytoplasmic) is often overlooked. A growing number of examples show that non-nuclear genetic elements are involved in reproductive isolation either because they coevolve with the nuclear genome that they are associated with or because they have conflicting evolutionary interests. Discoveries of microbes that impair hybridization directly by causing cytoplasmic incompatibility or affect sex ratio are rapidly accumulating and found in a wide variety of arthropods, including many mites. Here, I will report on the identity and effects of intracellular microbes in spider mites (Genus Tetranychus). Based on molecular phylogeny of the ftsZ gene all microbes that cause cytoplasmic incompatibility belong to the genus Wolbachia and are closely related. Cytoplasmic incompatibility is typically observed between infected and uninfected mite strains. Natural and greenhouse populations of spider mites are polymorphic for the infection.The effect of Wolbachia on crossability between spider mite strains is variable; it ranges from no effect to mortality among fertilized (female) eggs, female sterility and hybrid breakdown. In addition, Wolbachia affect fecundity of infected female mites compared to uninfected female mites.

Quorum Sensing, group selection and multicellularity.

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Gram-negative bacteria may sense local cell density though the secretion and uptake of autoinducer compounds belonging to the class of L-homoserine lactones. They may respond to density in ways beneficial to all members of the local bacterial population. This phenomenon, called "quorum sensing", forces reconsideration of theories of group selection, with populations divided into patches of available resource, and competing on a local level.

Interaction between cells in bacterial populations can be viewed as analogous to those between competing individuals in a population or, alternatively, as analogous to those between cooperating cells in a multicellular organism. Which of these two paradigms is more appropriate depends upon the expected degree of relatedness of the interacting cells, which, for clonal populations such as these, can best be quantified by the expected number of cells initially invading a patch of resource. Some population structures will favour wild-type cells when in competition with cells capable of quorum sensing, if the latter undergo a metabolic cost. Other structures favour the evolution of quorum sensing.

Inter-plant communication and anti-herbivore defense

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When damaged by, for instance, herbivorous insects or mites, plants can defend themselves via (increased) production of toxic compounds or deterring substances. In addition to this direct defense, they can also defend themselves indirectly, via enhancement of the effectiveness of members of the third trophic level. One way of achieving the latter is through induced production of volatile chemicals. Hence, damaged plants can signal the presence of prey or hosts to the natural enemies (predators, parasitoids) of the herbivores.

Since these signals are volatile they will also reach downwind undamaged plants. Laboratory experiments revealed that plants which are exposed to volatiles from spider-mite infested plants gain protection against possible future infestation, in that 1) they become attractive to predators of the spider mites, and 2) the oviposition rate of spider mites is reduced on exposed plants. An active role of signal-exposed plants in their enhanced protection against herbivory remains to be proven. I will discuss some experiments aimed at elucidating the role these plants play.

Comparative analyses of microsatellite and mtDNA markers: Holarctic differentiation in the Arctic charr (*Salvelinus alpinus* L.) complex

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Arctic charr, *Salvelinus alpinus* L. (Teleostei; Salmonidae), has long intrigued biologists as a prime example for population differentiation and speciation in northern fishes. It exhibits a complex mosaic of variability in morphology, coloration, ecology, and life history traits. Paradoxically, genetic studies using traditional markers and approaches revealed little or no genetic differentiation among morphs, separate populations, and even subspecies.

We recently demonstrated the usefulness of microsatellite DNA in addressing evolutionary and conservation issues in Arctic charr from the central Alpine region of Europe. Here, we extended microsatellite DNA analysis, inferring evolutionary relationships among most taxa from the circumpolar Arctic charr species complex. In addition, variation in mtDNA from same populations was assessed by sequencing six hundred bases of the control region. Results of the two approaches are compared, and discussed for consistency with previous RFLP and allozyme data, and current systematics from morphological studies.

Mitochondrial DNA phylogeny of Brimstone butterflies (genus *Gonepteryx*) from the Canary Islands and Madeira.

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Part of the mitochondrial Cytochrome Oxidase I gene was sequenced for seven species of *Gonepteryx* (Pieridae) butterflies. Four of the species are island endemics inhabiting the Canary Island archipelago and Madeira. The remaining three are European and African conspecifics. Sequence data were analysed phylogenetically by maximum parsimony and maximum likelihood methods. The trees were used to deduce Canarian species' ancestry, sequential inter-island colonisation and the systematics of the group. The results suggest an African ancestry for the Canary Island taxa and a colonisation pattern, within the archipelago, compatible with the geological ages of the islands and other Canarian fauna: a colonisation sequence from Africa to Tenerife and Gomera, followed by Tenerife to La Palma. Contrary to some morphology based classifications which distinguish only two Canarian species, the molecular phylogeny indicated that there are three Canarian endemics, *G. cleobule*, *G. palmae* and *G. eversi* from Tenerife, La Palma and Gomera, respectively.

Host races of the anther smut fungus Microbotryum violaceum are different species

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The pollinator-borne anther-smut fungus Microbotryum violaceum is a parasite of many species of the family Caryophyllaceae. In all species affected by this disease the fungus has the same general effects. Diseased plants are sterilised when the fungus invades the flower buds and sporulates in the anthers, interupting normal microsporogenesis, also reducing female sexual organs and rendering them infertile. The species status of the different host races of this disease has been the subject of debate for a long time, with some authors splitting the nominal species M. violaceum into different groups of host races. Recently, on the basis of spore ultrastructure all host races were lumped within M violaceum.

We developed microsatellite markers to investigate patterns of gene flow and differentiation among the various host races of this fungal disease collected from 13 different host species growing in central Europe, mostly from the Swiss Alps. Microsatellite variation revealed almost perfect isolation among the host species studied, suggesting that barriers to gene flow exist.

Observations of insect visitors, the vectors for infectious spores, showed that in mixed sympatric populations of several host species, pollinating insects are largely constant, moving more readily between two individuals of the same species than switching species. This indicates that pollinator specialisation provides a first barrier to free genetic exchange among potential hosts of this fungus, allowing further specialisation on particular host species with associated evolution of reproductive isolation. Patterns of conjugation behaviour between haploid spores from different host races also revealed that reproductive isolation is partial among sympatric host races from different host plant species.

Adaptive changes in *Plasmodium* life histories in response to intervention strategies

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Strategies of resource allocation which maximise fitness can differ between benign and stressful environments. Consequently, natural selection often favours phenotypic alteration of reproductive effort in response to stress. In disease-causing organisms, such alterations could render intervention strategies against parasitic diseases less effective than anticipated. Malaria parasites (*Plasmodium* spp.) are capable of adaptively increasing the proportion of within-host replicating parasites (asexuals) that develop into non-replicating transmission stages (gametocytes) when conditions are unfavourable. Increased investment into transmission stages should therefore be expected following a variety of antimalarial intervention strategies, such as chemotherapy and vaccination. The results of controlled experiments *in vitro* and *in vivo* were broadly consistent with this hypothesis.

EVOLUTION OF THE NEO-Y CHROMOSOME IN BULGARIAN PAMPHAGIDAE GRASSHOPPERS

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Similar to the some Pamphagidae grasshoppers from the Caucasus and Central Asia (Bugrov, 1996), karyotypes with 2n=16+neo-XY (male) and 2n=16+neo-XX (female) have been found in four Pamphagidae species: *Asiotmetis limbatus, Paranocaracris bulgaricus, Paranocarodes shopardi*, and *Paranocarodes straubei* from Bulgaria as result from mutual translocation of originally acrocentric sex chromosome and medium size autosome.

The initial stage of the heteromorphization of the neo-Y has been found in *Asiotmetis limbatus*. In this species the neo-Y chromosome and the XR arm of the neo-X chromosome appear isomorphic and they exhibit a chiasmata during meiotic prophase.

Due to the extensive heterochromatinization of the neo-Y chromosome in *Paranocaracris bulgaricus, Paranocarodes shopardi* and *P. straubei* the sex mechanisms determination of its species seems to be a terminal steps in evolution of neo-Y chromosome in Pamphagidae grasshoppers.The one from possible causes of the evolution the sex chromosomes is the chiasmata decreasing between the initially homologous the XR arm of the neo-X chromosome and the neo-Y chromosome.

Species specific DNA: an open question

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MOLECULAR GENETIC SPECIES CONCEPT (MGSC)

Organisms whose genomic DNA differs in of above 10% overall mutation rate constitute separate species. Noncoding DNA as compared to genes seems to be crucial in making species separate because it more subject to mutation. The importance of an environment in keeping species separate is to manage genomic mutation rate with help of selection pressure.

A SPECIES SPECIFIC DNA

Species specific DNA can be regarded as DNA showing no homology in a sequence to any DNA in the genome of related but separate species. This homology can be resolved by means of common DNA hybridization. Genomes of related but separate species unquestionably contain species specific DNA. It may present DNA featured by a high intrinsic mutation rate or affected by random genetic drift both followed by weak selection. Its duty is still open problem. No data known show its relation to speciation.

A CAUSE FOR SPECIATION

Following strategies both are equally possible in causing speciation:

- suddenly a high overall mutation rate (which is generally low) followed by random drift or transitory dropped selection;
- constant but unequal (regarding different loci) mutation rate followed by selection until the threshold in mutation amount will be reached (possible indicator is species-specific DNA happened).

The first in above may be due to different things (e.g., replication/reparation machinery unbalanced by mutations, changes in environment or by foreign DNA).

Now the tools to indicate overall mutation rate became available - UP-PCR and related techniques (RAPD-PCR, AP-PCR, DAF etc.). Its features regarding species evolution are subject matter to talk about. The main outcome of the use of UP-PCR is the finding a comedown trend in total mutation rate from prokaryotes (bacteria) and simple eukaryotes (protozoan, yeasts/fungi) to high eukaryotes.

Microsatellite diversity in asexual and sexual isolates of the solitary parasitic wasp*Venturia canescens* Gravenhorst (Hymenoptera : Ichneumonidae).

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Venturia canescens Gravenhorst exists as an obligatory thelytokous (asexual) species of cosmopolitan distribution, and also as an obligatory arrhentokous (sexual) strain in southern France and Israel. We have cloned and sequenced 678 microsatellites from the asexual isolates which display an unusually strong bias to dinucleotide repeats with very few tri- or tetranucleotide repeat motiffs. Additionally, almost all the microsatellites are small ($n < 10$) and most (76%) contain inserts. They show little polymorphism within or between different geographical isolates or from samples collected at the same region over several years, supporting their stability.

However, the larger (principally $[GT]_n$) microsatellites do display considerable polymorphism between isolates and variance in repeat length can be detected within the same isolate after several generations. As expected the estimated mutation rate per loci is dependent principally upon the repeat unit length and absence of inserts.

In contrast, these microsatellite loci show greater repeat unit size and diversity in the sexual isolates of this wasp. Moreover, the estimated mutation rates for these loci, although also dependent principally upon the repeat unit length and absence of inserts, are greater than that for the corresponding asexual strains.

Moreover, this comparison is strengthened by the ability to induce asexuality and genomic homozygosity through artificial stable transfection of parthenogenetsis-inducing *Wolbachia* lines. These lines may then be maintained asexual, or cured by antibiotics, and thus represent an interesting model to study recombination and mutation (slippage) rates at microsatellite loci, and the role of spermatogenesis compared to oogenesis in generation of hereditable microsatellite polymorphism.

Venturia canescens **Gravenhorst: A model for the investigation of evolutionary selection of mating strategies under complimentary sex determination?**

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The solitary endoparasitoid *Venturia canescens* Gravenhorst was shown recently to also exist in southern France and Israel as an obligatory arrhentokous (sexual) strain which is subject to single locus-complimentary sex determination (sl-CSD). Diploid males develop to imago but are essentially, if not totally, sterile.

In contrast to the northern temperate Ichneumonids of the Campopleginae tribe studied so far (*Diadegma* genus), this southern temperate species displays mating strategies consistent with that expected under selection to avoid inbreeding. That is it is protandrous and upon eclosure females display a strong phototactic response and mating refractoryness, presumably allowing dispersal away from brothers. Moreover, females were found to strongly discriminate against copulations with siblings and frequently, but not always, against non sibling sex allele related males.

However, under optimised laboratory conditions, males although polygynous were found to be sperm limited in that a single copulation did not provide females with sufficient sperm to allow a continued sex allocation of 45-50% resulting in sperm depletion and male biased sex ratios. Moreover, following multiple mating males often were sterile, and male ferility decreased dramatically with age even in the case of virgin males. Following polyandry first male sperm precedence is normally the rule.

Whilst in the absence of field derived data this may be a reflection of the pausity of hosts normally parasitised in the field by this species as compared to the laboratory conditions, the implications of sex determination selecting upon mating strategies and sex allocation in southern and northern temperate Ichneumonoid species will be discussed.

Venturia canescens **Gravenhorst: an old friend with a new tale of sex determination.**

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The solitary thelytokous (parthenogenetic) endoparasitoid *Venturia canescens* Gravenhorst was shown recently to also exist in southern France and Israel as an obligatory arrhentokous (sexual) strain which is subject to single locus-complimentary sex determination (sl-CSD). Under laboratory conditions homozygotes at the sex locus developed to imago as diploid males at a constant elevated temperature; but at lower temperatures frequently, although not always, they developed as (homozygotic) females. The apparent temperature sensitive homozygotic sex determination was characterised to a 16 hour time-window covering the mid *ova* to early first instar developmental period, and found to show a mendelian inheritance. Thus, this allows the formation of genetically identical diploid males or females that are homozygotic at the sex loci with an unknown degree of genomic heterozygosity from crosses with the appropriate isofemale lines. Comparison of these, with hemizygotic haploid males and thelytokous females allows a molecular insight into the sex determination locus of sl-CSD in Hymenoptera. Moreover, this comparison is strengthened by the ability to induce genomic homozygosity through artificial stable transfection of parthenogenetsis-inducing *Wolbachia* lines, allowing the formation of genetically identical homozygotic diploid males or females.

This notion is further supported by analysis of two heterozygotic (diallelic, single locus) microsatellite loci which are conserved in other parasitoids of the Campopleginae tribe (Ophioninae : Ichneumonidae) with sl-CSD and thus may act as molecular markers for the sex determination locus.

This model and the data to date in elucidation of the molecular mechanisms of genetic and temperature dependent sex determination in Hymenoptera (CSD) will be presented.

Whither the diploid males? A study of single locus complimentary sex determination in three Ichneumonid parasitoids across the UK.

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The solitary endoparasitoids *Diadegma chrysostictos* Gmelin, *Diadegma fabricianae* Horstmann and *Diadegma armillata* Gravenhorst are subject to single locus complimentary sex determination (sl-CSD). Diploid males developed to imago and copulated with females, but are sterile and induced pseudovirginity.

In contrast to evolutionary expectations, females showed no mating discrimination against sibling, sex allele related ("cousins"), or diploid males. In contrast first male, and to a weaker extent, diploid male sperm precedence was usually observed following polyandry.

Imago and parasitised hosts were collected from field sites across the UK during 1994 to 1996 and the level of diploid males, virgin females and pseudo-virgin females was determined as was the number of alleles at the sex locus within each separate geographical population.

Field derived females were found to have mated to sex allele related males in up to 8.5% (south England, 14-16 sex alleles) to 23% (north Scotland, 4-6 sex alleles) of samples, yet very few virgin females, pseudo-virgin females, or diploid males were caught in any of the locations studied, and only rarely were diploid males reared out of field collected parasitised hosts. In the laboratory homozygotes at the sex locus developed as diploid males only at constant elevated temperatures, but principally as (homozygotic) females at lower temperatures more akin to that experienced in the field in these locations. Thus, for this to be a valid explanation of the rarity of diploid males in the wild would necessitate the existence in the field of females homozygotic at the sex locus. Utilising two microsatellite and one minisatellite loci, in conjunction with data from laboratory cultures, we show preliminary evidence to support the existence of sex locus homozygotic females in the field in the UK, especially at the isolated northern limits of their range, and so at least partially validate the temperature model. In which case, perhaps the interest focuses upon whether if sl-CSD is still conserved within non temperate region Ichneumonids, and if so has the avoidance of sibling mating evolved in these species?

Effective size and polymorphism for populations under selection and linkage

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The general theory of effective population size (Ne) is extended to cover linkage under selection. Ne is a function of the rate of reduction of the covariance between neutral and selected genes generated by finite sampling. This reduction depends on three factors : the recombination rate, the reduction of variance in both selected and neutral genes due to drift, and the change of variance of the selected genes due to selection. An infinitesimal model (an infinite number of genes of infinitesimally small effects) is first considered, making the third factor to be irrelevant. If the mapping function of Haldane is assumed and the density of genetic variance is uniformly distributed on chromosomes, simple approximations of the effective size can be achieved for additive and multiplicative gene actions,

$$Ne = \frac{N}{1 + C^2\, Ne / L} \quad \text{and} \quad Ne = N \exp(-C^2\, Ne / L)$$ respectively, where

N is the census size of the population, C^2 is the genetic variance for fitness (individual fitness measured relative to the mean fitness) and L is the genome size in Morgans (the sum of the sizes of all the chromosomes). When large gene effects are involved, deleterious (background selection) and favourable mutations are considered separately, as changes in variance due to selection are different for both models. The essence of the argument allows to show how the magnitude of the drift process is smaller for recent neutral mutations than for the old ones. The reduction of Ne affecting to a neutral mutation is progressive until the asymptotic value is reached after a number of generations. Genetic diversity, measured either by the mean heterozygosity or the proportion of segregating sites, is the result of the contributions of neutral mutations in previous generations, which depend on the values of Ne in consecutive generations.

Developmental stability and physiological condition of barn swallows *Hirundo rustica* (L.) during the breeding season

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Linking developmental stability to physiological condition and fitness allows assessment of how environmental conditions mechanistically affect the development of phenotypes and the consequences of such phenotypes for reproductive success. Environmental stress can have severe effects on organisms, resulting in reduced developmental stability (measured as fluctuating asymmetry), and poor physiological condition, which can decrease reproductive output and the chances for survival. As aerial foragers and long-distance migrants, barn swallows are highly sensitive to environmental stress. There is considerable evidence that different kinds of stress are equivalent because they affect basic biochemical and metabolic processes. Then barn swallows that were stress resistant during moult in winter, and thus have low flight feather fluctuating asymmetry, are expected to be stress resistant during the breeding season as well, and to be in good physiological condition. In addition, barn swallows with low fluctuating asymmetry and good physiological condition are expected to have the highest reproductive success. Barn swallows of known breeding status were repeatedly sampled during the breeding season. Generalized linear models were used to analyse the relationships between indicators of condition, wing and tail fluctuating asymmetry and reproductive success, independent of sampling date within the season. Body mass, hematocrit and serum cholesterol level, as indicators of good physiological condition, were positively related to reproductive performance, as expected. However, the relations of condition indicators with fluctuating asymmetry were less clear.

Genetic variability and phylogenetic relationships among populations of two endemic Spanish species of *Barbus* (Cyprinidae) inferred from RAPD-PCR analysis.

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In the last decade, a variety of DNA fingerprinting techniques has become available and has been applied in different fields of genetic studies. The development of arbitrary primer directed DNA amplification methods allows the examination of genomic variation without previous knowlegde of DNA sequences.

These methods have been sucessfully used to detect genetic variation in related species and populations, and for differentiation and identification in a great variety of organisms.

In the present work, we have applied the RAPD-PCR technique to genus *Barbus*. The genus *Barbus* is a freshwater group widely distributed throught the Iberian Pensinsula where seven out of its eight species are endemics. Classifications of such species are based on morphological characters but this group presents small differences either among populations and species. Besides this, no studies involving their genetic structure are still made based upon DNA fingerprinting.

Taking into account the above considerations, we have analysed six populations of fishes belonging to *B. bocagei* and *B. sclateri* species applying the RAPD-PCR technique. Results are discussed in relation to both: first, the genetic structure of this two endemic spanish species and the problem of their systematics and identification; second, the sensitivity of the RAPD-PCR technique for the study of the genetic relationships in fishes group.

Lack of cytonuclear disequilibria and evidence of natural selection in the evolution of mtDNA in two natural populations of Drosophila subobscura

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In order to detect the existence of interactions between mitochondrial (mtDNA) and nuclear DNA, cytonuclear disequilibria analyses have been carried out in two natural populations of Drosophila subobscura from Majorca and Minorca islands (Spain). As in other populations analysed previously, restriction analyses of mtDNA revealed two main haplotypes, I and II. Moreover, the Minorca population showed a higher number of rare haplotypes than the Majorca population. Ten allozymes were used that were selected according to a varied degree of functional relationship with electronic transport chain where several mitochondrial gene products are involved. Cytonuclear disequilibria tests between haplotypes I and II and nuclear enzymes were carried out following Asmussen and Basten (1994, Genetics 138:1351-1363). No significant disequilibria were detected. Although the enzymes selected could not be the appropriate one, the lack of disequilibria could suggest that the evolution of both haplotypes is independent of the nuclear genome. Other evolutionary forces, different from hitchhiking, could also be invoked to explain the pattern of haplotype distribution observed.

Evidence of mtDNA non-neutral evolution was observed after performing the Tajima's test. Both populations showed a significant departure from neutrality, what might be interpreted as due to either a change in population size, which it seems not to be the case, or to purifying selection.

These results are compared with previous ones on mtDNA evolution of experimental and natural populations of the same and related Drosophila species.

Sexual reproduction and genetic variation in Allium vineale

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A number of species in the genus Allium have the potential capacity for both sexual and asexual reproduction. The inflorescences of these species contain two types of reproductive organs; flowers and bulbils. The flowers are the sexual reproductive organs and will produce progeny that is genetically variable, while the bulbils are the asexual reproductive organs, producing progeny that is genetically identical to the parent.

One such species is A. vineale, common in Europe and western Asia. Natural population of A. vineale typically show a large variation in the ratio of flowers to bulbils in the individual inflorescences, It is common to find, within a single population, individuals producing different proportions of sexually produced offspring, from 0 to 100 %. This proportion differs significantly between populations.

Seed-set is regular and does not vary between populations, indicating a trade-off between sexually and asexually produced offspring in this species. Genetic variation for the proportion of sexually produced offspring was estimated using cloned progeny. Genetic diversity within and among populations was further estimated using RAPDs and compared with the sexual outcrosser A. schoenoprasum.

Intron patterns in ancient duplicated genes support the exon theory of genes

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Genes for chloroplast and cytosolic glyceraldehyde-3-phosphate dehydrogenases of eukaryotes (class I GAPDH) are descendants of an ancient gene family that probably originated in the progenote. During eukaryotic evolution both genes were transferred to the nucleus from the progenitors of present-day chloroplasts and mitochondria, respectively, thereby replacing preexisting GAPDH genes of the host cell. Chloroplast-specific GAPDH genes from nuclear genomes of landplants, green algae and *Euglena* contain introns at 12 different positions, six of which coincide precisely and two others approximately with intron positions found in glycolytic GAPDH genes from landplants, algae and animals. These findings together with observations that introns tend to correlate with GAPDH protein structure strongly support the exon theory of genes suggesting that introns may be as old as the genes in which they reside. The data further demonstrate a lineage-specific loss of introns, in addition to "slippage" and "sliding" of introns in different GAPDH gene regions.

Relevant publications:

1. Kersanach R, Brinkmann H, Liaud MF, Zhang DX, Martin W, Cerff R: Five identical intron positions in ancient duplicated genes of eubacterial origin. Nature 367:387-389 (1994).
2. Cerff R, Martin W, Brinkmann H: Origin of introns-early or late? Nature 369, 527-528 (1994).
3. Henze K, Badr A, Wettern M, Cerff R, Martin W: A nuclear gene of eubacterial origin in *Euglena* reflects cryptic endosymbioses during protist evolution. Proc Natl Acad Sci USA 92: 9122-9126 (1995).
4. Cerff R: The chimeric nature of nuclear genomes and the antiquity of introns as demonstrated by the GAPDH gene system. In Go M, Schimmel P (eds.) Tracing Biological Evolution in Protein and Gene Structures, pp. 205-227. Proceedings of the 20th Taniguchi International Symposium, Nagoya, Japan. Elsevier Science, Amsterdam (1995).

The Evolution of Sex and the Molecular Clock in RNA Viruses

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We show that when laboratory populations of the RNA virus ϕ6 are subjected to small bottlenecks and hence intensified genetic drift, they experience a decline in fitness. This outcome confirms that the average effect of mutations is deleterious and it is used to support the possibility that Muller's ratchet can operate in these viruses. Muller's ratchet is the hypothesis that sex evolved in response to drift and a high deleterious mutation rate. The advantage of sex is that it helps recreate through genetic exchange genomes with fewer or no mutations. However, the operation of Muller's does not alone guarantee an advantage of sex. It is additionally necessary that the deleterious mutations that have accumulated through drift are not allelic. We have crossed populations that have been subjected to drift and find that hybrid viruses can recover fitness through mutations. However, they recover an additional amount over the contribution of mutations. This additional amount shows that the deleterious mutations are likely not to be allelic and it represents the advantage of sex to ϕ6. We argue that these combined results provide indirect support for an advantage of sex through Muller's ratchet. We also propose that evidence or the lack of evidence for a molecular clock in two RNA viruses, influenza A (a sexual virus) and VSV (an asexual virus), provide additional support for Muller's ratchet, and Ohta's model of molecular evolution by slightly deleterious mutations.

Reproductive conflict in fruitflies

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Conflict between males and females is an issue of central importance in evolutionary biology and can occur at all levels from behaviour to molecules. In *Drosophila melanogaster*, sexual conflict is caused by male accessory gland proteins (ACPs) transferred with sperm at mating. ACPs increase the reproductive success of males relative to females, which is suggestive of an evolutionary arms race between ACPs and their receptors in females.

ACPs have behavioural and physiological effects on females. They increase egg-production by the female, reduce her receptivity to further matings and disable the sperm of her previous mates. They also elevate her death rate, presumably as an evolutionary side effect. In addition, ACPs show high rates of evolutionary change. There is a growing realisation that this type of covert molecular sexual conflict is pervasive.

The effect of deleterious mutations on variation and evolution at linked loci

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Background selection is the process by which the selective elimination of recurrent deleterious mutations at one or more strongly selected loci affects variation and evolution at a neutral or weakly selected linked locus. A model is presented of the effect of background selection on molecular variability in Drosophila melanogaster. It is argued that much of the observed relation between rate of genetic recombination and level of DNA variability in this species can be explained by background selection. The interaction of background selection with other modes of selection, such as balancing selection and local selection, is explored.

CHEVILLON C. Wed 27 Aug S16 C. CHEVILLON

A comparison of mtDNA control region sequences and their restriction polymorphism for native Panamanians and Mongolian

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Polymorphic mtDNA markers have been used extensively to investigate human phylogeography, but their high rate of recurrent mutation (and homoplasy) make interpretation notoriously difficult. It has been shown that not all homoplasic ambiguities are aquivalent; some are less harmful for phylogeographical conclusions (Excoffier et al. 1992, Bandelt 1995). We pursued that idea by investigating relationships between the degree of polymorphism, the rate of homoplasy and the impact of resulting ambiguities along the evolutionary network

We used a collection of 279 humans from Mongolia and Panamá, for which mtDNA diversity was defined by both Dloop sequences and RFLPs, *i.e.*, two non-overlapping sets of markers in the same mitochondrion. Dloop nucleotides were ranked according to their degrees of polymorphism, and included one by one in analysis. At each step of this progression, we checked the partition of Dloop diversity among RFLP strata and populations, as well as the correlation between the two distance matrices.

Three main results emerged: **(1)** the two data sets make mutual sense, but coherent translation between Dloop and RFLP information is not trivial. **(2)** the most polymorphic D-loop characters are the most correlated with the RFLP characters, but the maximum correlation is only about $r = 0.60$. **(3)** the most polymorphic (most informative) sites are also the most mutable and homoplasic: they represent both the signal and the noise.

These results suggest the need for wider and more general discussions on the relative strenghts and weaknesses of alternative approaches to using mtDNA markers for intra-specific phylogeographic purposes.

CIANCHI R. Sun 24 Aug S20 R. CIANCHI

Molecular phylogeography of European plethodontid salamanders

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mtDNA variation has been investigated in *Hydromantes* plethodontid salamanders to clarify phylogenetic relationships among the taxa of this genus. Inferred phylogeny has been used to test the validity of a paleogeographic scenario explaining their current distribution, based on allozyme data.

Hydromantes are the only plethodontid salamanders living in Europe, and their range includes central and north-western Italy, French Maritime Alps and Sardinia . Allozyme studies have already shown that three species live on the mainland (*H. italicus*, *H. ambrosii* and *H. strinatii*) and four are found in Sardinia (*H. flavus*, *H. supramontis*, *H. imperialis* in the Eastern side of the island, and *H. genei* in the South). Allozyme, karyologic and cytomolecular data strongly support a closer relationship between Eastern Sardinian and mainland taxa than between the former and the Southern Sardinian *H. genei*, in spite of their geographic proximity (Nascetti *et al.,* 1996; Nardi, 1991; Nardi *et al.*, 1997).

A phylogeny of the genus has been inferred using partial sequences of the mitochondrial cytochrome b gene from all the *Hydromantes* taxa, in order to explain the geographic and genetic patterns. The data show three main clusters: mainland taxa, Eastern Sardinian species and *H. genei*. *H. ambrosii* populations are gathered in two geographically and genetically well characterized sub-clusters, as to are *H. genei* samples. The results obtained are in general agreement with those from other approaches. The combined results support the hypothesized paleogeographic scenario correlating the separation of the ancestors of the three main *Hydromantes* groups with the events leading to the disjunction of the Corsica-Sardinia microplates from the continent.

State dependent allocation to growth, reproduction and repair

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The dynamic programming model was developed to study optimal resource allocation to growth, reproduction and repair of somatic damage, which were assumed to appear during whole life with constant rate. Damage, if not repaired, accumulated leading to increased mortality rate and decreased resource acquisition rate. Hence organism's physiology deteriorates the model involves ageing,. but ageing is an outcome of optimal allocation decisions.

The optimal strategy was followed through the entire life from birth until death. The allocation strategy was found to vary with individual age and it was optimal to invest resources to growth early in life and then to cease growth and start reproduction. Repair, if undertaken at all, was found to be the highest early in life, declined later on and ceased before death. The optimal allocation strategy was depended on the extrinsic mortality caused by external environmental factors imposed on the organisms. Under hazardous environment it was optimal to allocate higher proportions of resources into growth and reproduction which resulted in high growth rate, high reproduction rate early in the reproductive life which diminishes constantly due to negative effect of damages accumulated. In contrast, low levels of environmental mortality favored high proportion of resources allocated to repair and in consequence slow growth and increasing reproduction following maturity which decreased in advanced ages.

Changes in the frequencies of non-metric characters during the period of low abundance in Apodemus flavicollis and A.sylvaticus populations.

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Non-metric traits on rodent skull do not directly cotribute to fitness of an individual, and therefore, they are probably subject of the neutral evolution. Moreover, most of non-metric traits are not sex and age dependent. In this study, variation in 7 non-metric traits of 510 *A. flavicollis* and 494 *A. sylvaticus* trapped in a suburban forest on the periphery of Prague during the years 1987-1993 was analyzed. Effects of species and time on individual traits were examined and age, sex, season and skull asymmetry were the other factors analysed in order to might be excluded their influence on time changes. All traits exhibited differences between species, three traits were age dependent, one trait was sexually dimorphic. No traits exhibited directional asymmetry.

In each species four traits were affected by considerable rapid changes in time. These changes were expressed as differences between low abundance years (or preceding peak) and consecutive periods. This phenomenon can be interpreted as an evidence for rapid genetic changes associated with the population depression. The concrete mechanisms likely to be acting in the local conditions are discussed.

Pathogens and Plant Life Histories

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Age-specific patterns of survival, growth and reproduction represent adaptations of plant populations to local environmental conditions as constrained by their phylogenetic history. Pathogens affect plants indirectly through selection on particular life history traits and directly by phenotypic alteration of the same traits. The potential role of pathogens in selecting for plant growth form (unitary or clonal), mating system (outcrossing, selfing or apomixis) and dispersal mechanism (temporal and/or spatial) is discussed and illustrated with selected examples. Alterations of plant life histories resulting from pathogen infection are also considered with special focus on the systemic fungus Atkinsonella hypoxylon infecting grasses in the genus Danthonia. A comparative study of four host species has revealed a general trend for infected plants to exhibit greater survival and vegetative growth compared to uninfected conspecific, but decreased seed production and a shift from a mixed mating system to complete selfing. These changes are interpreted in terms of conflict between optimal pathogen and plant life histories.

Modeling Survival of Stresses and Regeneration of Damage in Trees.

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The ESS investment of limiting resources for survival and regeneration of storm stresses is modeled for long lived trees. Several versions of the basic model without regeneration are analysed, which include the benefits of increased survival and regeneration of damage, the cost in reproduction, and the effects of the distributions and timing of the stress in the population. There are important differences between the effects of synchronized vs. unsynchronised stresses in the population. With synchronized stresses, there is no single ESS. A wide range of investments is stable against different rare investment strategies. The ESS investment in survival of unsysnchronized stresses increases if stress independent mortality decreases, and if the cost of the resistance decreases. The optimal investment may increase or decrease when the probability of more extreme stresses increases.

The fitness of each individual increases if the allocation of resources for resisting stress is adapted to its local stress probability distribution. This adaptation depends on the information each individual gets, which is highly uncertain for rare extreme stresses and for short exposure times.

The ESS investment in the regeneration of damage is zero if the initial marginal benefit of investment in resisting the stress is greater than the marginal benefit of investment in regeneration. The opposite case is also possible: the optimal investment in resistance is zero if the initial marginal benefit of investment in resisting the stress is smaller than the marginal benefit of investment in regeneration. There is a possible wide range of optimal investment in both resistance and regeneration.

The results of the model can be applied to a wider class of organisms, stresses, and resistance and regeneration mechanisms.

Homeobox genes in the Collembolan *Folsomia candida*

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The hexapods originated from an arthropod ancestor at least 500 million years ago. Hexapods are distinguished from other arthropods on the basis of a distinct body plan with three tagma; a head with mouth parts and antennae; a thorax with three pairs of legs and, sometimes, wings; and a limbless abdomen. The origin of the hexapods from an ancestral arthropod, and the evolution of the distinct hexapod bodyplan, are not well understood. The Collembola are primitive wingless hexapods that occupy one of the most basal branches in the hexapod phylogentic tree. Some features of the development and morphology of Collembolans do not conform exactly to the canonical insect Bauplan. For example, the organization of the Collembolan abdomen is different from that of "true" insects: Collembolans have only 6 abdominal segments compared with 11 or 12 in most insect groups, and most of those segments have appendages that appear to be modified limbs.

The morphological differences by which we define various animal groups arise during the development of each animal from a zygote. The distinct segmental organization of each arthropod group, including the hexapods, is in large part controlled by a family of regulatory genes known as Hox genes. The Hox genes are arranged in a linear cluster along the chromosome, and their order on the chromosome is the same as the order in which they are expressed, anterior to posterior, during development. The Hox gene cluster has been extensively studied in *Drosophila melanogaster*, and some work has been done in other insects, but no work has been done in any of the more basal hexapod groups.

We shall report on a characterization of the Hox cluster in a Collembolan, *Folsomia candida*. We have completed a primary PCR screen to identify Hox genes and we are now generating more structural information on the individual genes, and on the cluster itself.

Is asexuality reversible in *Andricus* gall wasps?

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In general, asexuality is associated with lower taxa - the tips of evolutionary trees - and we assume that it is an irreversible state (although microbe-induced parthenogenesis in some parasitoid wasps can be "cured). We investigated changes in reproductive mode in *Andricus* gall wasps using a phylogenetic approach. Individual *Andricus* species may be sexual only, asexual only, or have seasonally alternating sexual and asexual generations. We used mitochondrial DNA data to estimate the phylogeny of 30+ European species of *Andricus* and related cynipid wasps. Mapping mode of reproduction onto the phylogeny results in some clades that are predominantly asexual, but include a single, apparently derived, sexual species. If this interpretation is correct, sex loss is reversible in *Andricus*. However, we must consider two important alternative explanations. First, it is possible that some supposedly asexual "species" have a sexual generation in other parts of their range where they are less well-studied. Second, it is also possible that our European collecting efforts undersampled some older sexual species that are found in the Asian centre of diversity. Whichever of these explanations proves correct, it is clear that sex is a labile character in *Andricus* wasps.

Transposons as clade markers for their hosts

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The selfish interests of transposable elements may often conflict with those of their host genomes. However, we argue that transposons may actually help evolutionary biologists to reconstruct the phylogenies of their hosts. Because integrated transposon sequences are passed vertically to daughter host species, the integration events can serve as strong indicators of host monophyletic clades. In this respect their use is analogous to that of gene duplications in deep phylogeny. However, integration events may be informative about much more recent speciation. Several different integration events may be needed to estimate species phylogenies but, in contrast with DNA sequence data, the analysis may often be straightforward. One drawback is the need to distinguish orthologous markers (derived from speciation events) from xenologous markers transferred horizontally between species and paralagous markers amplified within one genome. Fortunately, sequence comparisons, integration site comparisons, and congruency tests can all be used for this purpose. We discuss this novel approach to phylogeny using data on transposable elements in animal genomes.

COOK M. Wed 27 Aug P5 M. COOK

Influence of parasite life history on host clutch size

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Fitness strategies which might be selected for in a host interacting with parasites are studied.

First, the effect of epidemic type attacks by a parasite to which all host genotypes are susceptible is considered. The host could evolve one of two strategies to maximize fitness, either to lay a large clutch from which most young are successfully raised in epidemic free breeding seasons, but virtually no young during epidemics, or to lay a small clutch from which most young are raised in all breeding seasons. Fewer demands would be made, for example, of a female laying a small clutch or feeding a small brood. A protected polymorphism of the two fitness strategies, if genetically determined, is possible. Both strategies together allow for a higher longterm geometric mean fitness than either strategy on its own.

Second, the attack by a parasite consisting of two strains to each of which there is a resistant host genotype is considered. The host could evolve the strategy of laying medium size clutches from which most young are raised in breeding seasons when the relevant virulent parasitic strain is rare, and a few young in seasons when the virulent strain is common. Again a protected polymorphism is possible. Both fitness genotypes together allow for a higher longterm geometric mean fitness than either genotype on its own, and for smaller fluctuations in population size. With frequency dependant selection the strategy can still be successful if there is some randomness in the system.

Comparative phylogeography and postglacial colonization routes in Europe

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The Quaternary cold periods in Europe are thought to have heavily influenced the amount and distribution of intraspecific genetic variation in both animals and plants. The phylogeographies of ten taxa, including mammals (*Ursus arctos*, *Sorex sp.*, *Crocidura suaveolens*, *Arvicola sp.*), amphibians (*Triturus sp.*), arthropods (*Chorthippus parallelus*), and plants (*Abies alba*, *Picea abies*, *Fagus sylvatica*, *Quercus sp.*), were analysed to elucidate general trends across Europe. Only a small degree of congruence was found among the phylogeographies of the ten taxa, but the likely post-glacial colonization routes exhibit some strong similarities. A Brooks parsimony analysis of these intraspecific data produced an unrooted area-phylogram, showing that (i) the northern regions were colonized generally from the Iberic and Balkanic refugia, and (ii) the Italian lineages were often isolated due to the presence of the Alpine barrier. The comparison of colonization routes highlighted four main suture-zones where lineages from the Iberic, Italian, and Balkanic refugia meet. Some of the intraspecific genetic distances among lineages indicated a pre-quaternary divergence that cannot be connected to any particular cold period, but are likely to be related mainly to the date of arrival of each taxon in the European continent. As a consequence, molecular genetics so far appears to be of limited use in dating Quaternary events.

Historical biogeography of two competing shrews of the genus *Crocidura* inferred from mt DNA variation.

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Historical biogeography studies based on mt DNA variation are usually restricted either to a single species or to the comparison of a number of unrelated species within a given region in order to elucidate general trends. To date few studies were devoted to competing species whereas competition plays a major role in structuring species distribution and genetic variation.

The population genetic structures of two shrews which enter into competition when in syntopy, *Crocidura suaveolens* and *C. russula*, were examined by sequencing parts of the mt DNA cyt b gene in individuals from localities scattered over their European range. Genetic structures were very different between both species suggesting different histories. *C. suaveolens* exhibited high levels of haplotype diversity arguing for a long-term presence of the species within its present range. The major phylogenetic subdivisions occurred between populations from each side of the Alps in concordance with the location of Quaternary cold refugia in Spain and in Italy-Balkan. At the opposite, *C. russula* genetic variation was very low suggesting a founder effect resulting from a recent colonization of its European range likely from southern Spain. Genetic and distribution data suggests that the Alps have proved an effective barrier to migration for both species and that the western lineage of *C. suaveolens* has recently suffered a huge range reduction probably in relation with *C. russula* invasion.

The study demonstrates that the temporal prospect provided by molecular approaches highlights the effect of intraspecific competition upon the historical biogeography of extant species.

The genetic basis of the trade-off between calling and wing morph in males of the wing dimorphic cricket, *Gryllus firmus*

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Alternate morphologies exist in a wide range of species. A commonly encountered dimorphism in insects is wing dimorphism, in which one morph is winged, has functional flight muscles (LW) and is flight-capable while the other has reduced wings (SW) and cannot fly. *Gryllus firmus* is a wing-dimorphic cricket found in the southeastern USA. Although there are well established phenotypic trade-offs associated with wing dimorphism in female crickets, no such trade-offs have been demonstrated in male crickets. In addition there only exist two studies that have established a genetic basis to trade-offs to macroptery; these studies have only been on females crickets as well. The prediction is that LW males, since they have to expend energy to maintain the flight apparatus, will call less and therefore attract fewer females than SW males. In addition the traits involved in the trade-off; time spent calling, wing morph, and wing muscle condition, should all have measurable heritabilities and all be genetically correlated. Differences between morphs in male *G. firmus* in the likelihood of attracting a female were tested in the laboratory using a simple T-maze where females chose between a LW male and a SW male. Time spent calling for each male was recorded on the sixth day of adult life. SW males attracted 63% of the available females while LW males attracted 37% (P=0.01). A significant difference in time spent calling was found between SW and LW males (SW=0.86±0.01, LW=0.64±0.01 hours). A regression of female choice against the absolute proportional difference in calling time between males revealed that, as the difference in calling time between males increased, the likelihood of a female choosing the longer-calling male also increased . All the traits of the trade-off had significant heritabilities (call=0.72±0.13; wing morph=0.22±0.07; muscle weight=0.47±0.22); the genetic correlations were also significant (call & wing morph=-0.46±0.20 for SW, -0.68±0.16 for LW; LW call & muscle weight=-0.32±0.09). Therefore the trade-off to macroptery is probably a primary factor in the maintenance of wing dimorphism in male *G. firmus*.

Parthenogenesis in *Aphelenchus avenae*: is an endosymbiont involved?

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Aphelenchus avenae is a cosmopolitan soil nematode exhibiting both amphimictic and parthenogenetic populations. *Wolbachia*, are well known cytoplasmic endosymbionts of arthropods which can cause cytoplasmic incompatibility and cytoplasmically induced biased sex-ratios in the hosts. Although *Wolbachia* and other bacteria symbionts are known to be widespread in insects and other arthropods, little is known about its presence in other invertebrate groups. In nematodes there is a single report of a *Wolbachia*-like micro-organism; ultrastructural evidence for bacterial symbionts is more widespread which may point to *Wolbachia*-like bacteria being quite common in nematodes as it is in arthropods.

A. avenae exhibits a reaction to temperature common to *Wolbachia* infected arthropods: at high temperatures males emerge in a fully parthenogenetic population. In this work we consider the possibility that evolution of asexuality in *A. avenae* is the consequence of a genomic conflict between the worm and its endosymbiotic bacterium which manipulates the cytogenetics of its host for its own ends. A PCR-based assay using primers specific to *Wolbachia* and *Erlichia* produced a positive result. We are repeating the PCR using different primers followed by sequencing to identify the symbiont. To test whether a *Wolbachia*-like symbiont is causing parthenogenesis in *A. avenae* we are "curing" parthenogenetic nematodes of the bacterium by heat shock and antibiotics. If the evolution of *A.avenae*'s breeding system is, indeed, influenced by a bacterial endosymbiont, this would be the first case outside a few arthropod taxa.

Evolution of introns in Drosophila amylase genes

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In *Drosophila melanogaster*, the amylase gene *Amy* is an uninterrupted 1.5 kb coding sequence. In several Drosophila species, however, it had been previously shown that a short intron was present. We have investigated the distribution of this intron in more than 150 Drosophilid species and found that most of them had a short intron at the same position, in a conserved region of the *Amy* gene. Its size was generally 60-80 bp but reached 750 bp in some species. In other insects, the same structure was evidenced. Moreover, there is an intron at the same position in vertebrate amylase genes. We propose that this intron could predate the divergence between insects and vertebrates. We have also evidenced a number of independent intron loss events in various Drosophila lineages, including *D. melanogaster* itself.

In the divergent related gene *Amyrel*, there is no intron at the predicted position but there is a short one at an unexpected position, which suggests that it was inserted after the *Amy*/*Amyrel* duplication.

Plant competition experiments: The condition for coexistence and estimating the probabilities of the different ecological scenarios

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Based on the classical two-species plant competition experiments, the condition for coexistence assuming hyperbolic response functions and constant seed survival probabilities was examined analytically. Using the found condition for coexistence and Bayesian statistics, the probability of the four possible outcomes of two-species competition (coexistence between species one and two, species one always outcompete species two, species two always outcompete species one, and either species one or two will outcompete the other depending on the initial conditions) can be estimated. The probabilities of the different ecological scenarios were estimated in a competition experiment with *Avena fatua* and *A. barbata* (Marshall and Jain, 1969).

The balance of nature between opposite, dualistic and complementary processes

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The study of complex systems, has shown that simple interactions sometimes lead to very complicated structures and behaviours. Conversely, complex interactions can lead to simple patterns. This is particularly true for systems poised at a 'critical point' where the distribution of two or more phases become scale invariant. We can look many evolutionary, ecological and behavioral dynamics in the spirit of a "computer game" between opposing complementary processes. Simple computer simulations based on cellular automata with only two cells states (active and receptive) are able to reproduce many features of these dynamics. The most interesting systems are generated when an active cell can both induce the adjacent receptive cells into activity (binary dissociation) and induce the adjacent active cells to the receptive state (binary association). These simulations suggest that analogous morphogenetic laws underlays the evolution of physical and biological systems. At the molecular level, the evolutionary dynamics of chemical systems are the result of the competition between entropic catabolic reactions, degrading chemical compounds, and neg-entropic anabolic reactions, increasing the complexity and the configurational order of material structures. Successful evolution requires the right balance between entropic and neg-entropic processes, innovation and conservation, internal self-organisation and external natural selection, specialization and plasticity, differentiation and homogenization, competition and cooperation. The equilibrium between these opposite processes leads to the formation of fractal patterns which increase their complexity during the phylogenetic and ontogenetic development. Also the geographical and taxonomic distributions of living organisms follow power laws. The fractal structures are typical of the most adaptable "homeodynamical" systems working at the border between order and disorder. In this scenario, the evolution of life on the Earth is not a fortuitous event, but the unavoidable result of the self-organising properties of natural structures.

Polygenic mutation rates for fitness traits in nematodes

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Estimates of the evolutionary consequences of spontaneous mutations on fitness are used in many areas of biology, including theories relating to the evolution of sex and recombination, evolution of ageing, mutation load and the conservation of small populations. Previously, a mutation accumulation experiment in *Caenorhabditis elegans* (Keightley and Caballero, *Proc. Natl. Acad. Sci.*, in press) has provided an estimate for the rate of decline of fitness due to fixation of new mutations, two orders of magnitude smaller than that implied by the classic *Drosophila* experiments of Mukai and collaborators. Reasons for the differences between the two sets of observations are now being investigated.

It is unlikely that *Drosophila* and *C. elegans* have significantly different rates of mutation, as the rate of recessive lethal mutations measured appears to be similar in each. Another possibility is that the controls used in Mukai's experiments were flawed, making the results unreliable (Keightley, *Genetics* (1996) **144**: 1993). One other difference between the experiments was that the *Drosophila* viability was assayed in competitive conditions, which was not the case with the *C. elegans* experiments. It is possible that these stressful conditions are more likely to reveal fitness differences between lines and so could explain the different results of the experiments. We are now testing the *C. elegans* mutation accumulation lines and controls (which have been cryo-preserved) in different conditions to determine whether such interactions occur in harsher conditions, and thus see whether this can account for the differences observed, or whether other explanations such as lack of valid controls in the *Drosophila* experiments must be found.

Comparitive genome mapping between *Arabidopsis thaliana* and *Arabis petrea.*

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Cardaminopsis petrea and *Arabis lyrata* probably represent one species of different locations, because (1) they can be crossed, (2) the sequence of the Adh-locus was fairly similar, and (3) differences in microsat-alleles between populations of *Cardaminopsis petrea* were as large as differences between *Arabis lyrata* and *Cardaminopsis. petrea*. We will call the species here *Arabis petrea*. *Arabis petrea (lyrata)* and *Arabidopsis thaliana* are both members of the Brassicaceae family, tribe Arabidea (based on cpDNA data).

Species within the Brassiceae differ in chromosome numbers. There does not seem to be a correlation between classification and chromosome number, and the basic chromosome number of the ancestor is unknown. Both increase by duplication of chromosome segments, or decrease in chromosome numbers after polyploidisation may have occurred during evolution. Comparison of chromosome segments of *A. thaliana* (2n=10; 0.3 pg) and *A. petrea* (2n=16; 0.5 pg) may reveal some of the evolutionary background of the species. In this study markers of *A. thaliana* will be mapped in *A. petrea*. Five research groups collaborate in order to cover the five chromosomes of *A. thaliana* at intervals of 10cM. A preliminary study was done with six CAPS markers (cleaved amplified polymorphic sequence) in a F1 analysis. These six CAPS were located on each arm of three chromosomes in *A. thaliana*. Possible linkage between two CAPS of one chromosome indicated that the two arms still are linked together in *A. petrea*. A second study was based on isozyme markers both species. Comparison of linkage groups between the two species may reveal some of its evolutionary history.

The evolution of reaction norms and density-dependent number regulation.

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Quantitative genetic models of the evolution of phenotypic plasticity indicate that in a predictable and constant environment the optimal reaction norm will evolve under natural selection, apart from considerations of constraints. Quantitative genetic models ignore any influences of the numbers of individuals in the population. Numerical processes however influence the evolution of an optimized reaction norm, that is only identical to the optimal reaction norm under specific conditions.

DE JONG T.J. Sun 24 Aug S2 T.J. DE JONG

How geitonogamous selfing affects sex allocation in hermaphrodite plants

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Does the mode of self pollination affect the evolutionarily stable allocation to male vs. female function? I distinguish the following scenarios. 1) An 'autogamous' species, in which selfing occurs within the flower and prior to opening. The pollen used in selfing is a constant fraction of all pollen grains produced. 2) A species with 'abiotic pollination', in which the selfing occurs when pollen dispersed in one flower lands on the stigma of a nearby flower on the same plant. The selfing rate increases with male allocation but a higher selfing rate does not mean a reduced export of pollen. 3) An 'animal-pollinated' species with geitonogamous selfing. Here the selfing rate also increases with male allocation. When a pollinator transfers pollen between flowers of the same plant, many pollen grains are lost. As a result of this loss, pollen export to other plants in the population is a decelerating function of the number of simultaneously open flowers. In this model the selfing rate correlates negatively with pollen export (pollen discounting).

In all three models selfing selects for increased female allocation. For model 3 this goes against the general opinion that geitonogamous selfing does not affect the ES allocation. In model 3 and in model 2 with low levels of inbreeding depression, hermaphroditism is evolutionarily stable. In model 2 with high inbreeding depression the population converges to a fitness minimum for the relative allocation to male function. Once the population has arrived at this value, all mutants have higher fitness than the resident, corresponding with accelerating fitness gain curves.

If the selfing rate increases with plant size, this is a sufficient condition for size-dependent sex allocation (more allocation towards seeds in large plants) to evolve. I discuss the mechanism behind selection for female-biased allocation and the relevance of results for size-dependent sex allocation in plants and the evolution of dioecy.

Symbiotic bacteria in Western Flower Thrips (*Frankliniella occidentalis*).

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Symbiosis between insects and microorganisms is a wide spread phenomenon, and can be parasitic or mutualistic. Mutualistic interactions have been described in many insect systems, ranging from very tight associations like bacterial mycetomes in Homoptera to facultative symbionts in gut lumen. Symbionts can play a role in host plant adaptation by supplying essential nutrients or detoxifying toxins. In Homopteran species a strong correlation exists between phylogeny of the host and of the symbiont. We investigate if a correlation exists between genotypes of gut microbes and the use of food plants by the insect host. Western Flower Thrips is used as model system. This is an important pest insect, which has recently expanded its geographic distribution and host plant range. We study the role of bacteria in thrips adaptation to new host plants.

We have isolated bacteria from the thrips hindgut and midgut and cultured them on artificial medium. Analysis of 16s rDNA sequences and biochemical tests showed that these bacterial strains are all closely related Enterobacteriaceae. By means of RAPD markers it was confirmed that these bacteria were constantly associated with the thrips culture in our lab during a long period of time. The same RAPD markers were used to compare symbiotic bacteria in thrips populations from different countries and various host plants. Genetic variation found in thrips bacteria was very low.

The role of symbionts was studied using antibiotics. It was shown that the effect of the symbionts on thrips fitness depends on the food source of the thrips. Transmission of bacteria to larval thrips takes place via the food source. Strong correlation exists between bacteria in the mothers and in the offspring.

The Marketplace of Social Services in Primates: Simple and Complex Mechanisms of Reciprocity

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A *service* is an action that benefits another individual at a low or no cost to the performer. Grooming is a typical service among nonhuman primates, as is willingness to participate in sex or share abundant food. Most agonistic support also falls under this definition rather than under the more demanding definition of altruism. The distribution of services was investigated in chimpanzees (*Pan troglodytes*) and brown capuchin monkeys (*Cebus apella*). In both captive studies food-sharing occurred reciprocally, i.e. the rate of sharing by individual A with B correlated positively with that of B with A. All adult-adult combinations among 13 capuchins were tested pairwise in a situation in which food could be transferred through a mesh constraint. Males shared more with other adults than did females, and rules of reciprocity seemed to apply only to females. Possibly, males share as a parental investment strategy, whereas females do not. The simplest explanation of female reciprocity seemed symmetry. If food-sharing is produced by a combination of affiliation and social tolerance, and if affiliative preferences are mutual, this automatically results in a reciprocal distribution of the service.

In the chimpanzee study, however, we were able to exclude symmetry-based reciprocity. An earlier study had shown that food sharing was reciprocal, and that this correlation persisted after correction for symmetrical relationship characteristics. A new study of the same colony involved extensive data collection on spontaneous grooming followed by provisioning of large bundles of foliage to the twenty chimpanzees. The analysis of 6,972 food interactions among nine adults demonstrated that a) previous grooming facilitated subsequent sharing between the same individuals, b) the sharing increase was exclusively in the direction opposite to that of the grooming (i.e. after A groomed B, B shared more with A), and c) the sharing increase was highly selective, i.e. A's grooming of B did not affect B's sharing with other adults. This is the first evidence for sequences of partner-specific service exchange in nonhuman primates.

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Poster Abstract Title:

Segregation Distorters in the fungus *Podospora anserina.*

Spore-killers are segregation distorters found in several ascomycete fungi. In *Podospora anserina* spore-killing can be identified by the abortion of two of the four dikaryotic spores within the ascus. In the post-meiotic phase the spore-killer allele prevents the formation of spores not containing the spore-killer allele. In case of a cross-over event, ascospores end up with a 'killer' and a 'sensitive' allele. The ascus contains then the normal amount of four spores, the sensitive allele is 'saved'. The further the spore-killer allele is localised from the centromere on a chromosome, the higher percentage of four-spored asci within a fruiting body, and the less efficient the killer-gene. Backcrosses of the heterokaryotic spores from four-spores asci with the parental strains reveal that the sensitive alleles remain undamaged by the spore-killing action.

At the moment seven different types of spore-killer genes can be identified in *P.anserina*, of which 6 recently isolated from nature. The newly isolated Psk7 killer is apparently identical to a French killer strain originating from 1969. All spore-killer types can be distinguished from each other by killing percentage, localisation on linkage groups, and killing interaction among each other. Some sort of linear killing order or dominance seems to exists, when different killer types are crossed with each other. Still most of the natural population consists of strains sensitive to spore-killing, coexisting with the spore-killer strains. No resistant strains have yet been found nor fixed killer genes. Meiotic drive elements only work within an outcrossing population, however *Podospora anserina* is a secondary homothallic fungus, and mainly reproduces by selfing.

Genetic differentiation in the Galápagos caterpillar hunter *Calosoma granatense* (Col., Carabidae).

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Galápagos caterpillar hunters (*Calosoma sp.*) are specialized carabid beetles of which 4 species are known to occur in Galápagos. *Calosoma granatense* Gehin, 1885, is to be found on virtually every island of Galápagos, predominantly in the lowlands. It flies regularly because of its partly arboreal way of life in search of caterpillars. On younger volcanoes of the archipelago, *C. granatense* also occurs at higher elevation and shows wing polymorphism. The three other Galápagos *Calosoma* species are true endemics, limited each to the higher parts of a single island and possibly derived from the lowland species in convergent habitat shifts.

In order to test hypotheses related to the evolutionary ecology and adaptive radiation of these Galápagos caterpillar hunters, morphological, ecological as well as biochemical data are required. In this contribution, data on different biochemical markers are used to test the hypothesis that *Calosoma granatense*, although mostly possessing a high dispersal power, shows significant levels of genetic differentiation between populations. Both allozyme data (studied by cellulose acetate gel electrophoresis at five polymorphic presumptive loci) and preliminar mtDNA-sequence data (COI-region) are used. In general, the results confirm the mentioned hypothesis. The observed population genetic patterns have implications for conservation biology and are described in view of the relative importance of different underlying evolutionary processes, as well as in relation to isolation in space and time between different islands in the Galápagos archipelago.

Direct detection of length polymorphisms (DDLP), or how to get new genetic markers in three days in any species.

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Direct Detection of Length Polymorphism is a new protocol that take advantages of the efficiency of the AP-PCR method for the study of virtually every species in Population Biology. This protocol can detect DNA polymorphisms and lead to sequence information recovery from any genome in only two days; then these data can be used to design primers for mono-locus amplifications in population samples. Furthermore, the selected loci are "a priori" known to be polymorphic whereas the loci picked by the screening of a genomic library may not be. In addition, the use of a family in the first step of detection allows a direct test of the alleles transmission, as well as a detection of polymorphisms associated with some precise traits or deseases. In Population Genetics studies, this method was used to detect diagnostic and microsatellite DNA loci. However, it could be applied in many other fields of the Biology, such as in the definition of new STS. Again the use of a family allows an early mapping of the markers and the selection of the interesting ones. It could also be very useful when very closely related genome must be compared : genetically selected strains, transformed cell lineage...
Finally, this approach can be used whenever global comparison between two related genomes must be performed.

Oviposition strategy and fitness in the chestnut weevil, *Curculio elephas* Gyll. (Coleoptera : Curculionidae)

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In phytophagous insects, optimization of oviposition strategy by natural selection may lead to two major types of clutch sizes : isolated and clumped. Optimal clutch size depends on trade-offs such as number vs. size of offspring, number vs. offspring weight and survival.

In the chestnut weevil, *Curculio elephas*, females oviposit inside chestnuts and larvae are forced to feed and develop within a fruit chosen by their mother. Although one female can lay on average 28 eggs, in natural conditions, 55 and 28% of the infested fruits contain respectively one and two eggs. This result shows that a female lays only one or two eggs in each chestnut in at least 83% of cases and disperses her eggs in several fruits. By controlling the number of females and chestnuts in protected sleeves, we increased larval density per fruit in natural conditions. Our aim was to estimate costs and benefits of an oviposition strategy producing clutch sizes of one or two eggs per host. To test the influence of quantity and quality of resource (volume of chestnut, larval density per fruit and exit rank of larvae from the chestnuts) on fitness components such as weight, survival rate and fecundity of the emerging females, larvae were studied from the moment when they left the chestnuts to their transformation into adults . We found that an oviposition strategy of dispersion of eggs in several fruits has a greater fitness (in terms of growth rate) than a clumping strategy.

DEWILDE S. Thu 28 Aug S19 S. DEWILDE

Invertebrate globin gene structure.

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Conservation of intron location in gene families across widely divergent phyla and there separation of the genes in structural and/or functional coding domains is used as a proof for intron antiquity and for the exon theory of genes (1). However conservation of intron location is less conserved as it is generally claimed and they do not always separate structural and/or functional coding domains (2).

We determined the size and position of the introns in the globin genes of an annilid (*Aphrodite aculeata*), a mollusc (*Biomphalaria glabrata*), an insect (*Gastrophilus intestinalis*) and a trematode (*Paramphistomum epiclitum*).

Each of these genes displays an unprecedented characteristic different from the expected intron pattern or location. *Aphrodite* has a single G-helix intron (G7.0) and no B-helix intron . The absence of the latter suggests that the loss of introns is rather a stochastic event than caused by a single conversion.

Biomphalaria contains an additional intron in the A-helix (A3.2) next to the expected B12.2 and G7.0 introns. This extra intron may possibly be considered as a “precoding” intron. *Gastrophilus* displays two introns (D7.0; G7.0) where no introns were expected. Finally *Paramphistomum* has two introns in the positions B12.2 and G7.0. Assuming that trematodes are more ancient than nematodes we would expect here a three intron/four exon pattern (additional E-helix intron).

As such it is clearly demonstrated that neither the pattern nor the intron location is conserved in the globin genes studied.

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Dispersal and population structure in the Collared Flycatcher (Ficedula albicollis) on the island of Gotland: what can microsatellites tell us?

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The Collared Flycatcher (Ficedula albicollis) is a migratory passerine bird breeding mainly in eastern and central Europe and wintering in southern and central Africa. Two isolated populations inhabit the baltic islands of Gotland and Öland, c. 500 km north of the nearest continental populations. Most yearlings tend to return to their natal woodland or its vicinity, but dispersal distances between natal site and first breeding site may vary (partly because natal dispersal is sex-biased, females moving on average farther from their natal sites as compared to males. In this study we analysed the effects of natal dispersal on the genetic structure of flycatcher populations on Gotland using a combined approach of molecular biology (using DNA microsatellites) and population genetics (analysing gene flow and genetic differenciation between a geographical range of study populations on Gotland, taking a Hungarian population as external group). The results are compared with dispersal estimates from ringing data. The evolutionary consequences of natal dispersal are discussed.

Developmental commonality in annelid segments and bryozoan modules: a heuristic approach.

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Early in the 20th century, biologists were faced with the Herculean task of explaining how evolutionary modifications in ontogenies produced evolutionary novelties in adults. It appeared self-evident that quite different ontogenies, giving rise to diverse adult morphologies, would have different genetic bases.

Following a paradigm shift in developmental genetics, we enter the 21st century faced with a question partly the converse: how do evolutionary changes in similar, seemingly conserved genetic systems produce such a bewildering array of ontogenies and adult morphologies? The problem now, although somewhat better defined, remains Herculean.

Here, I do not argue any sort of strict developmental homology between annelid segments and bryozoan modules. My goal is rather to explore how developmental commonality between the two might provide insights into the origin of modular organization in bryozoans. To do so, I draw an analogy between continuous development in the polychaete worm *Ctenodrilus serratus* (which is segmented and cyclically modular) and growth in a bryozoan colony (which is modular but lacks overt segmentation). As a heuristic device, a column of zooids within a bryozoan colony, beginning with the ancestrula and continuing linearly to the peripheral growth zone, is compared to the succession of segments of the annelid, beginning with the head and ending with the teloblastic growth zone. In this comparison, astogenetic changes in zooid morphology furnish an analogy to segmental differentiation.

Work is underway to understand the role of Hox and segmentation genes in the transition from a segmental to a modular organization in *Ctenodrilus*, and this may provide insights into the origin of bryozoan modularity. Very little is known about the developmental genetics of bryozoans. However, scattered reports of astogenetic mutants among bryozoans provide an intriguing, relevant source of data. Ultimately, the measure of our understanding of the evolution of development will be how well we can use existing information to predict the roles of developmental regulatory genes in previously unstudied organisms.

Phylogenetic reconstruction of the Caribbean reef coral genus *Madracis*.

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Coral species are highly variable taxonomic units displaying variation in morphological, ecological and possibly genetic characters. This often causes problems in identification which is a necessary prerequisite for many ecological studies. The Caribbean coral genus *Madracis* Edwards and Haime has a large distribution and shows a broad range of ecological and morphological variation within and between putative species. Here we show preliminary results of phylogenetic relationships between *Madracis* species inferred from ITS1, 5.8S and ITS2 sequence variation. Additional data sets based on morphometric and ecological data will be generated and analysed both independently in a "total evidence" approach. The ultimate goal is to reassess the systematics and, using an historical ecological approach, discriminate evolutionary constraints from contemporary adaptation. This will in turn set the stage for population level studies.

Phylogeny and molecular evolution of Delphacid planthoppers.

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The mitochondrial cytochrome oxidase subunits I, II and III have been sequenced and the suitability of these subunits for phylogeny reconstruction has been investigated for different taxonomic levels within the family Delphacidae. Maximum parsimony and Neighbour-Joining produced the same rather well supported trees with subunit III. The trees showed a high level of congruence with an earlier published tree based on morphological characters. Using Neighbour-Joining subunit III seems to be useful from the species to subfamily level and possibly higher levels. Subunit II, and possibly subunit I, however, may be useful only at lower taxonomic levels. As shown in other studies, in closely related species transitions are more frequent than transversions. Patterns of substitution will be further analyzed and discussed.

Polymorphism of mtDNA structure in sugar beet plants with normal and sterile cytoplasms of different origins.

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Cytoplasmic male sterility (CMS) is one of the mechanisms of gynodioecy maintenance in higher plants. Combination of sterile cytoplasm with a nucleus carrying recessive genes restoring fertility in a cell results in normal (fertile) phenotype of plant. Recently it was shown that mitochondrial genome is responsible for CMS. Only two types of cytoplasms are known now in Beta vulgaris L. - normal (N) and sterile (S).

We studied the structure of mtDNA from plants of 30 lines with N and 15 with S cytoplasms by RFLP analysis, blot-hybridization with mt genes as the probes and the analysis of plasmid-like molecules. It was shown that all tested normal cytoplasms may be divided into 3 groups in accordance with their restriction patterns differing among each other. However, only weak polymorphism was detected among S cytoplasms. Moreover, the plants of three lines with converted cytoplasms (from N to S) had identical restriction profiles of mt DNA and the same content of plasmid-like molecules as their isogenous forms with sterile Owen's cytoplasm. The reasons of the higher extend of polymorphism of mt genome structure of sugar beet plants with normal cytoplasms than one of the CMS plants are discussed. The possibility of the coexistence of two types of mitochondria (N and S) in one plant is discussed.

t-haplotypes across the mouse hybrid zone in Denmark: smugglers or customs officers?

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The limited introgression of the sex chromosomes across the hybrid zone between *Mus musculus domesticus* and *M. m. musculus* suggests they play a major role in the genetic incompatibilities between the two subspecies. Autosomal genes are also likely to be involved, and the hybrid sterility gene *Hst-1*, and other genes on the proximal region of chromosome *17* are good candidates.

However, these genes all map to the *t*-complex region which exists in two forms, each with separate histories and different properties. One is the *t*-haplotype, a segregation distorter which in its present form appears to have spread through the subspecies after their divergence. Depending on the extent to which the *t*-haplotypes have co-evolved with the genomes of the two subspecies, they could either contribute to hybrid breakdown, or flow across the hybrid zone driven by its infectious properties.

To test these possibilities we have identified the mice carrying *t*-haplotypes in samples caught across a transect of the hybrid zone in Denmark using the *t*-specific markers, *Tcp1* and *Hba-ps4*. The *t*-haplotypes detected were then classified into different groups using variable microsatellite loci. The possibility of using the same loci to estimate the introgression of the genes on the same region of the wild type chromosomes was also investigated.

DORIT R. Tue 26 Aug S15 R. DORIT

In vitro evolution: adaptation at the molecular level

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We have explored the trajectories followed by different populations of ribozymes under selection in vitro for novel catalytic activity. Using both the Group I intron of Tetrahymena thermophila and the M1 ribozyme of E. coli as our model systems, we evolve replicate populations of these catalytic RNAs for improved cleavage activity on a DNA substrate. These experiments suggest that the evolutionary outcomes depend both on stochastic events occurring early in the experiments and on the canalization of the populations along specific trajectories. Our results provide a glimpse into the rugged underlying landscape over which these populations travel. In the case of the M1 ribozyme, we have also investigated the consequences of in vitro catalytic optimization on organismal fitness by transforming our in vitro ribozymes back into the E. coli cell. The results point to the additional constraints and evolutionary pressures shaping the evolution of this catalytic RNA in vivo.

The genetic basis of phenotypic plasticity: Do plasticity genes exist or not?

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What is the genetic basis of phenotypic plasticity? Several authors have suggested that genetic variation for plasticity may be the real target of natural selection, rather than that for the trait mean. Consequently others have argued that two sets of genes must exist, one to influence the trait mean and another to influence the plasticity of the trait. If such genes exist there is no concensus over what kind of gene a plasticity gene would be. Technologies now exist to identify individual genes contributing to quantitative trait variation. If plasticity genes exist, than the positions of these genes, known as quantitative trait loci (QTL), can be mapped on the chromosomes and their individual effects on the phenotype quantified. Thus, the existence of plasticity genes can be either confirmed or rejected. If plasticity genes are found to exist and the exact QTL is known (not just a marker linked to a QTL) than questions about the nature of such genes and how they respond to selection can also be addressed. In this paper we report on what this approach has accomplished in several plant species, and our results for the plasticity of flowering time in *Arabidopsis thaliana*.

Why some animals have symbiotic micro-organisms

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Various animals bear symbiotic micro-organisms that possess a biochemically-complex metabolic capability absent from the animal. Those animals which gain access to such a capability derive nutritional benefit from the association.

This talk will explore the cellular and genetic bases of animal-mediated modification of microbial metabolism and transport systems that have underpinned the evolution of these intimate symbioses. Specific examples from recent research on photosynthate release
from symbiotic algae in marine invertebrates and amino acid production by symbiotic bacteria in insects will be included.

TRILLS IN BLUE TIT SONGS : A DISPLACED CHARACTER DUE TO COMPETITION WITH GREAT TIT ?

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Abstract:

Blue tits (Parus caeruleus), as many other species, show much geographic variation in their songs. Songs that include a trill (series of rapidly repeated notes) dominate the song repertoires of blue tits over a large geographical area on the European continent. By contrast, these songs with trill have never been reported in North Africa, the Canary Islands, and in some parts of the island of Corsica. The syntax of many blue tit songs without trill is similar to that of great tit (*Parus major*) songs, and dominate the song repertoires in populations where great tit densities are low. By contrast, the syntax of blue tit songs with trill differs much from that of great tit songs, and is especially observed in populations where great tit densities are high. Because in many populations, great and blue tits are in close competition for resources (e.g. nest sites), and blue tits are mostly dominated by the larger great tit, we suggest that the blue tits songs with trill are a result of a character shift in syntax to facilitate species recognition, and this to minimise interspecific territorial interactions with great tits. We present results of playback experiments which tested this hypothesis.

A hard life is always too short; an evolutionary argument for time limitation

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Most models of parasitoid foraging behaviour assume that parasitoids maximize their long term offspring gain per unit of time, which implies that the animals have unlimited egg supplies and hence are time-limited. Many parasitoid species, however, have limited resources. When animals die with eggs still in their ovarioles this would suggest that they would have done better if they had allocated more of their resources to longevity, especially when eggs are costly.

In this talk we explore a model that predicts the optimal allocation of resources with respect to survival and egg load for given egg costs (in terms of survival) in a variety of environments. The environments are characterized by different types of travel time distribution between patches and host distribution among patches.

The results show that in a wide range of the parameter space selection produces optimal genotypes that invest in egg loads larger than the mean number of hosts that individual parasitoids may expect to meet during their lives. Consequently, the majority of individuals in a population end up time-limited, even when egg costs are relatively high. The rationale of these results is that in a stochastic environment parasitoids with large egg loads that happen to land on a rich patch strongly contribute to the next generation. High rates of time limitation turn out to be associated with poor environments, where the mean encounter rate with hosts is low.

DUPAS S. Wed 27 Aug 'S6 S. DUPAS

Geographic variation in rates of immune reaction in a *Drosophila*-parasitoid system : the genetic and physiological mechanisms involved and the evolutionary forces operating.

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Leptopilina boulardi is an Eucoilid parasitoid from tropical and mediteranean regions mainly associated with *Drosophila melanogaster* as a host. It can however infest other species of the melanogaster subgroup. Most of of the species of this subgroup are restricted to tropical African regions. The parasite is therefore facing different situations in tropical Africa versus other regions. Furthermore, the suitability to parasitism by *L. boulardi* varies deeply among the different hosts of the *melanogaster* subgroup. This suitability is mainly determined by the ability of the parasitoid to suppress or counteract the immune reaction of the host (Carton and Nappi, 1997). Immune counteractive ability is therefore an essential trait to explain the effective host range of this parasitoid. In *L. boulardi*, this ability is due to virus-like particles produced by the parasitoid accessory gland and injected into the host during parasitization). Nevertheless, Dupas *et al* (submitted) demonstrated that the trait is genetically transmitted along the parasitoid chromosomes as a single segregating factor. This indicates, first that the virus DNA is integrated in the parasitoid chromosomes and secondly that from an evolutionary point of view the trait has to be considered as belonging to the parasitoid. Variations in the rates of immune reaction has been observed between localities (Carton and Nappi 1991). The authors noted that the rates of immune reaction in *D. melanogaster* are generally very low excepted in Brazzaville locality (tropical Africa) and we have also observed a high rate of immune reaction in Ivory Coast. **To explain the reduced immune suppressive ability of *L. boulardi* against *D. melanogaster* in tropical Africa, we propose a « gene for species » 0model in which each parasitoid immune suppressive gene is specific to a single host species and is counterselected when unnecessary (trade off ?).** To demonstrate host specificity of immune suppression, we compared different wasp strains on the different sibling host species. We observed first that the Congolese and Tunisian strain of parasitoid have different host-specificity within the melanogaster subgroup and secondly that these two host-specific immune suppressive systems are genetically unlinked. To test the trade-off hypothesis, we studied the evolution of immune suppressive genes in population cage experiments using specific host strains.

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Y. Carton and A.J. Nappi Acta Oecologica, 1991. 12(1), 89-104.
Y. Carton and A.J. Nappi, 1997. Parasitol. Today, 13 (in press).

Inbreeding and outbreeding in an intertidal copepod: mate choice and fitness consequences

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Inbreeding between close relatives generally reduces fitness while crossbreeding between populations may either decrease fitness or increase fitness. The intertidal copepod *Tigriopus californicus* provides an ideal model for understanding the mechanisms underlying breeding effects due to its short generation time, ease of husbandry, strong population differentiation and the accumulated evidence for inbreeding depression, hybrid vigor and outbreeding depression in various crosses.

To test for avoidance of extreme inbreeding, males were given a choice between sibling and non-sibling females from their own population. To test for avoidance of extreme outbreeding, males were given a choice between females from their own population vs. a genetically divergent population. Consequences of inbreeding were tested by measuring fitness components in offspring of full-sibling matings in several populations. Consequences of outbreeding were measured in a series of crosses between pairs of populations spanning a broad range of genetic distances, based on sequences of the mitochondrial gene cytochrome oxidase I. Fitness in parental populations, F1 hybrids, F2 hybrids and the first backcross generation were compared using a quantitative genetic model to tease apart the effects of gene interactions within and between loci.

Evolution in the greenhouse: a study on differential resistance to plant toxins in two races of a phytophagous mite

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Greenhouses in the temperate zone are true ecological islands for the two-spotted spider mite *Tetranychus urticae* Koch (Acari: Tetranychidae), a globally polyphagous herbivore. Studies have revealed adaptations to the greenhouse environment, such as loss of diapause, suppression of the tendency to disperse aerially and resistance to greenhouse-specific pesticides. In addition, rapid evolution of adaptation to new host plants, and especially to various greenhouse crops, has been demonstrated. Therefore one would expect that greenhouses provide an almost ideal constant environment for rapid radiation of host plant specific races.

Theory predicts host plant specialisation to evolve when the environment and the host resource are relatively constant. This prediction is based on the assumption that the generalist pays a cost for its flexibility ("Jack of all trades but a master of none"). Consequently, the specialists should show a trade-off in that improved performance on one host is associated with decreased performance on the other. The search for such trade-offs in many herbivore-plant systems has been largely unsuccessful, which has led some researchers to conclude that the trade-off assumption is not important in explaining host race formation. However, others have pointed out that specific requirements in experimental design have to be met to expect a trade-off to be found. We argue that there is a need to focus better on trade-off relations with respect to ecological key-factors in herbivore-plant systems.

We have studied the resistance to plant toxins of spider mite strains collected from tomato and from cucumber. Relative to cucumber, tomato is a particularly hostile host plant to many arthropod herbivores because of the toxicity and stickiness of secretions from glandular hairs covering stems, petioles and leaves. The most important toxin is a methyl-ketone, 2-tridecanone. It appeared that - upon instantaneous exposure to high doses - cucumber strains were more susceptible to this toxin than tomato strains. However, when the strains were first exposed to low doses and then subjected to a high dose, the cucumber strains exhibited increased levels of resistance, whereas the tomato strains did not. Apparently, the cucumber strains possess a flexible, induced resistance to the tomato toxin, while tomato strains have a fixed, constitutive resistance. We will discuss our plans to quantify the costs of induced resistance compared to constitutive resistance, in an attempt to measure this cost of flexibility.

The impact of the tri-phasic life history of red algae on the mating system : inbreeding and male gamete dispersal in *Gracilaria gracilis*

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Haplo-diploid species such as the red alga, *Gracilaria gracilis* have very particular life-history characteristics: (1) three types of individuals cohabit within a population : haploid male and female gametophytes and diploid tetrasporophtes; (2) there are three dispersal vectors : haploid spores, diploid spores and non-flagellated male gametes; and (3) fertilisations are followed by the formation of a cystocarp, inside of which the zygote multiplies mitotically, giving rise to thousands of diploid spores. The cystocarp is retained on the female thallus which therefore may play a role in the nurture and protection of the zygote. The consequences of this typical rhodophyte life history on the mating system, male reproductive success, and the dispersal of male gametes are explored in this study. Here, cystocarps were utilised in order to study the matings that take place in a natural population. Using two microsatellite loci as genetic markers, the genetic structure of two diploid generations (G_0 : *in situ* population and G_1 : cystocarps) was analysed and a paternity analysis was carried out on the cystocarps. We show that the matings are weakly structured within the study population. We also demonstrate that gene flow via male gametes is heterogeneous: one the one hand, it is limited to less than one meter within the population, but on the other hand, a considerable amount of exchanges between populations is revealed. Finally, male reproductive success is highly variable and correlated with the number of females a male mates with. Although male gametes are not flagellated in this species, they do not seem to be a limiting factor for female fertility. Sexual selection may operate in this population: males may compete with each other for access to females and/or females may choose among male mates.

Intraspecific variation in temperature/reproduction relationships in ectotherms and its consequences for size and number of offspring

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The physiological and genetical response of ectotherms to a temperature increase generally comprises a decrease in body size at each stage of development, including the egg stage. Although this phenomenon has been called "a biological law for ectotherms", the ultimate causation of both types of response is poorly understood.

We argue that a proximate explanation for the size - temperature effect will help to evaluate its evolutionary significance, and we have made an attempt to find such an explanation in studies of egg size in the carabid beetle *Notiophilus biguttatus* F., cultured at a variety of controlled temperature regimes.

Egg size shows a clear negative relationship with oogenesis temperature, betraying a difference in temperature sensitivity between the rate of follicle production and the rate of vitellogenesis. The difference between the temperature/performance curves for follicle production and vitellogenesis has profound consequences for the relationship between size and number of eggs. For example, if females vary in temperature sensitivity or in optimum temperature for reproduction, the correlation between size and number of eggs among females at a certain temperature will change from negative at low temperatures to non-existent at high temperatures. Experimental data were in agreement with the assumptions and predictions of this model, implying that responses to selection for offspring size and fecundity, achieved at a certain temperature, may follow from variation in temperature-performance relationships among the mothers.

We hypothesize that in ectotherms in general phenotypic plasticity in offspring size as a function of temperature depends on the temperature optimum for reproduction; if so, a response to selection for a change in plasticity may simply be a consequence of a change in optimum temperature.

EXCOFFIER L. Wed 27 Aug S16 L. EXCOFFIER

The effect of mutational hot-spots on mtDNA sequence polymorphism

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The effect of mutation rate heterogeneity on patterns of DNA polymorphism was investigated through simulation studies in stationary and expanding populations. Recent population expansions and mutation rate heterogeneity have overall similar effects on several polymorphism indicators, like the shape and the mean of the observed pairwise difference distribution, or the number of segregating sites. It follows that the size of population expansion may thus be overestimated when inferred from the mismatch distribution if nucleotides have dissimilar substitution rates. Population expansion and uneven mutation rates have however contrasting effects on Tajima's *D* statistic. Its consequence on Tajima's test of selective neutrality is investigated. The patterns of polymorphism of several human populations analyzed for the mitochondrial control region are examined. Substitution rates appear more heterogeneous in the second hypervariable segment of the control region than in the first segment. We also evaluate the possibility of detecting and identifying highly variable sites using an approach that does not require the reconstruction of phylogenetic trees. However, it appears difficult to quantify the respective contribution of past demographic history and uneven mutation rates from a single sampled evolutionary process.

Characterization, polymorphism, and inheritance of (AG/TC)n microsatellites in Taraxacum officinale

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The occurrence of diploid sexual and triploid apomictic plants makes *Taraxacum officinale* an interesting model for the study of the ecology and evolution of sexual and asexual reproduction. Such studies require information on gene flow between sexual and asexual plants, the genetic structure of clonal populations, and the genetic bases of apomixis. Genetic markers are then required, which have to be highly polymorphic, genetically informative, and convenient for large-scale population screening.

To produce hypervariable single-locus codominant PCR markers, we developed microsatellite markers in Taraxacum. A genomic library was screened for (AG/TC)n repeats and provided an average of one positive clone every 60 kb. Seventy-one percent of the positive clones sequenced contained a (AG/TC)n repeat with n greater than or equal to nine. Ten percent of them also showed (AC/TG)n or (AT)n repeats, suggesting some association between these different types of dinucleotide repeats.

PCR primers were designed in the regions flanking the repeats and are used to determine the length polymorphism of the microsatellites in sexual and asexual populations.

Segregation and co-segregation ratios of the microsatellites are also investigated in a sexual progeny to check for Mendelian inheritance and genetic linkage of the markers.

Microsatellite dynamics : evidence from genomic data

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We are investigating what can be inferred about microsatellite dynamics from the frequency of repeat arrays in the genomes of yeast, nematode and man.

Repeat sequences of 8 or more nucleotides are greatly over represented in all three species, compared to the expectation if the genome evolves only by point mutation. In contrast shorter sequences generally occur at approximately the frequencies expected. This is evidence for a threshold for dynamic mutation of approximately eight nucleotides, regardless of the core sequence.

The data from all three organism is broadly similar, but there are many interesting differences. For example, in the nematode the mononucleotide A sequences do not show the threshold like behaviour shown by other repeats, suggesting that dynamic mutation does not occur.

We have built a simple model in which genomic sequence evolves under the combined influence of point mutation and dynamic mutation, in order to establish what mutational processes could cause the observed patterns. This model has established that dynamic mutation causes an over representation of large repeats, compared to expectation, even if 50% of dynamic mutations reduce repeat number. The reason for this is that if the genome evolves by point mutation, then there will be many more short sequences than long ones, all of which will be prone to upward dynamic mutation.

We are now trying to estimate mutational parameters from the data. If it is assumed that the genome is at equilibrium, then the ratio of point mutation to dynamic mutation can be estimated from the extent of the over representation of large repeats.

Heterologous gene expression in *Escherichia coli* populations under stress conditions

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It is known that under selective conditions cell division is repressed but mutants crossing starvation barriers appear; this phenomenon has been called "directed mutation" or "adaptative mutation".

We have constructed a new system to study this phenomenon which is based on the use of a bacterial strain mutated in a gene x, containing a heterologous and potentionally functional , but promoterless, gene x onto the low copy number plasmid pAF58. Therefore this strain is phenotipically X^-, but if it is placed under (strong) selective pressure, i.e. the requirement of the function encoded by gene x, revertants X^+ may appear if a mutation generating a promoter upstream the plasmidic gene occurred.

For this purpose we have used the *Azospirillum brasilense his* operon (*hisBdHorf1AFEorf2)* which is not transcribed by the *Escherichia coli* RNA polymerase and thus is unable to complement the *E. coli hisA, hisB* and *hisF* mutations. When the bacterial population of *E. coli his* mutants containing plasmid pAF58 was placed in the absence of histidine, after at least two days of incubation at 37°C His^+ revertants, appeared. The frequency of His^+ revertants increased in time reaching the maximum after four-five days of incubation at 37°C and was strongly dependent on the number of bacterial cells plated, on the concentration of histidine in the plates, but was independent from cell growth phase. The genetic analysis performed on some of these revertants revealed that the His^+ phenotype was due to a mutation falling in a region upstream of the *A. brasilense his* operon and generating a promoter-like sequence which can be recognized by the *E. coli* transcriptional apparatus.

The experimental evidences suggest that this process might have played an important role during the early stages of cellular evolution, when ancestral organisms acquired new metabolic abilities by a massive genetic transfer by cell fusion (sinology) and/or by horizontal gene transfer (xenology).

On the cost of reproduction in long-lived birds; the influence of environmental variability

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Life history theory suggests that animals should balance their current investment in young against their chances to reproduce in the future. One fundamental prediction from the theory is that long-lived species should be restrictive in any increase of their current investment. It has been suggested that long-lived species have therefore have evolved a fixed level of investment in young in order to maximize their own adult survival. However, recent experimental studies have shown that long-lived seabirds have a flexible reproductive performance and adjust their effort in raising young both according to their own body condition and to the need of the chicks.

In this study we present a model on the optimal balance between reproductive effort and adult survival for long-lived birds breeding in a stochastic environment. During poor breeding conditions maximum fitness is achieved either by not-breeding at all or by, later, abandoning the brood. Beyond a certain threshold in breeding conditions there is a steep increase in reproductive effort and equally steep decrease in adult survival. The model is applied on two hypothetical long-lived seabirds differing in their potential fecundity. For the genotype with a potentially high fecundity, the model predicts a high threshold for breeding (i.e breeding condition need to be very good for the species to attempt breeding), and above the threshold, the value of reproduction in terms of fitness is high. For the genotype with potentially low fecundity, the model predicts a low threshold for breeding, and the value of reproduction in terms of fitness is low. By increasing the clutch-size in the model, we examine the optimal response to an experimental brood-size manipulation on the two genotypes. For both genotypes, the model predicts that the threshold for breeding is lower among controls than among enlarged birds, giving a range of possible outcomes of the experiment depending on breeding conditions. The few studies on brood enlargements in long-lived species carried out so far may support the predictions from the model.

FEDOROV V. Sun 24 Aug S20 V. FEDOROV

Mitochondrial DNA phylogeography and the evolutionary history of chromosome races of collared lemmings in the Eurasian Arctic

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Collared lemmings (*Dicrostonyx*) demonstrate extensive chromosome variation along their circumpolar distribution in the high Arctic. To reveal the history of this genus and the origin of chromosome races in the Palearctic, we studied geographic pattern of mtDNA variation by using eight tetranucleotide restriction enzymes. Lemmings were collected from much of the Russian Arctic during the 1994 Swedish-Russian Tundra Ecology Expedition.

The main split in mtDNA phylogeny is at the Bering Strait and corresponds to the main chromosome division between the Beringian and the Eurasian groups of karyotypes. Divergence estimates suggest that, despite the Bering Land Bridge, Palearctic and Neoarctic forms have been separated since the mid Pleistocene.

Five distinct phylogenetic groups of mtDNA haplotypes, corresponding to geographic regions, were found along the Palearctic coast. Low nucleotide and haplotype diversity and a star-like phylogeny within phylogeographic groups of haplotypes suggest regional bottleneck-events in the recent past, most probably, due to warming events during the Holocene. There is congruence between phylogeographic pattern of mtDNA variation and geographic distribution of chromosome races; 70% of the total mtDNA variation is allocated among chromosome races. This congruence implies that historical events such as fragmentation and allopatric bottleneck-events have promoted the origin of chromosome races in the collared lemming.

Mutation Models and Evolution of Microsatellites

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Several stochastic models for the mutation process of microsatellites are compared. Mathematical analysis and numerical evaluation of population statistics for these models suggest methods for estimating important evolutionary parameters. How sampling affects estimation is also discussed. The mathematical treatments suggest a simple test for heterogeneity among populations. A method for estimating the level of population subdivision is also proposed.

Floral heteromorphisms: Adaptive significance and developmental mechanisms underlying their evolution

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We discuss the adaptive significance of a number of intra-individual floral phenotypic polymorphisms (floral heteromorphisms), including floral color change, monecy, enantiostyly and various traits associated with mix-mating systems. In addition we discuss the evolution of developmental mechanisms which may underlie the evolution of floral heteromorphisms. We pay particular attention to the potential role of a breakdown of developmental homeostasis as the initial step in the evolution of heteromorphisms.

Density-dependence of deceptive species reproductive success: population dynamics and conservation biology.

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Many species of orchids are called deceptive as they do not reward their pollinators. Insects can be lured by mimicry (food model mimicry or sexual deception) but in some cases the deceptive plant does not mimick a precise model: pollinators, first attracted by floral display, are learning, while foraging, to avoid the deceptive flowers and to visit rewarding ones only. We study this pollination mechanism by modeling the pollinator behavior and investigate how it affects deceptive flowers reproductive success, population dynamics and survival of rare deceptive species.

The speed of pollinator learning is depending on how frequently they encounter a deceptive flower. Pollination efficiency of deceptive flowers is affected by the time it takes to a pollinator to stop foraging, either because it estimates it is not profitable or because sated. Reproductive success follows thus quite complex density-dependent variation.

The competition between deceptive and rewarding flowers for pollinators visits is simulated in a metapopulation model to predict the population dynamics. Equilibrium values of population sizes and extinction probability are calculated. Inferences on conservation biology of these species are drawn from these results.

Geographic variation in the sound producing wing structures of field crickets Gryllus bimaculatus: consequences for speciation theory.

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The harp area of cricket wings is involved in producing the calling song of field crickets: the size of the harp determines the carrier frequency of the call, a trait which is crucial for mate recognition in this species. A multivariate analysis of 24 morphological characteristics over a 400 km transect indicated that morphological traits not involved in the sound-producing organs had significantly larger loadings on the first component (explaining 45% of the total variation, second component 8%) than those of the harp area. This suggests that the morphology of the harp is much more stable than the other morphological traits measured. Calls from different localities on the transect were recorded under standard conditions in a sound chamber and there were no significant locality-based differences in the call frequency. However, significant locality-based differences still existed for the morphological characteristics of of the harp. In fact, a stepwise discriminant function analysis on all the individuals was successful in determining the locality of 97% of them. Even though the morphology of the harp is stabilised, geographically-based variation still existed but which is not detectable in the calls of crickets from different locations. Morphological stability of the harp is probably the result of natural selection. Modeling as well as statistical analysis did not indicate directional selection acting on these traits, leaving stabilising selection as the only alternative. These results are consistent with the predictions emanating from the recognition concept of species. We intepret hybridisation between *G. bimaculatus* and closely-related taxa, as well as the origin of reproductive isolation in these taxa. Our results are also discussed in the light of recent analogous findings on other taxa, including cricket frogs.

FERNANDEZ-ESCUD. I. Wed 27 Aug P15 I. FERNANDEZ-ESCUDERO

How to be successful if your are an ant in the Mediterranean high mountain

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The high mountain is a very peculiar and restricted ecosystem that obliges insects and other arthropods to develop special adaptations for survival.

In this work we present the study of different adaptation of *Proformica longiseta* Collingwood, 1978 (Hymenoptera:Formicidae), endemic species from the high mountain of southern Spain, inhabiting the Sierra Nevada (Granada, SE Spain) between 1900-2800 m in elevation. It occurs on in large open areas that climatically represent high-mountain steppe.

The active period of *P. longiseta* lasts only three and a half months, so it has to develop the brood in a short period. *P. longiseta* nests under rock with a certain size which provide the appropriate microhabitat for this purpose. In addition the queens develop the ovaries during hibernation, so they are ready to start laying at the beginning of the active period.

This species is active between 4.1-51.1 °C, so it can start the activity early in the summer and does not stop in the hottest days when the temperature of the soil reach 60 °C.

This species has replete workers, which store food for the end and the beginning of the active period when the food is very scarce.

P. logiseta is a polygynous species, this increases colony survival, because when the queen dies, the colony does not die. In addition the colony founding occurs by budding, which increases success of the new nests in a restrict habitat.

Molecular variation within and among rabbit populations: effects of domestication

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Using gene frequency data for 16 polymorphic loci (85 alleles), we conducted a phylogenetic analysis of a set of representative wild and domestic rabbit (*Oryctolagus cuniculus*) populations. The utilisation of various genetic distances and procedures of phylogenetic reconstruction showed the existence of two well differentiated population groups corresponding to the subspecies *O. cuniculus algirus* and *O. cuniculus cuniculus*. An asymmetrical distribution of the total genetic variability of the species was found to result from a higher number of polymorphic loci in *O. cuniculus algirus*, as well as from a higher number of alleles per locus, especially due to the occurrence of private alleles. The analysis of domestic breeds of various origins clearly showed that the present domestic rabbit populations were exclusively derived from the subspecies *O. cuniculus cuniculus*. The domestication process probably occurred very recently and was not associated to an important loss of genetic diversity. Recent molecular data greatly strengthened these results.

Restriction of male fertility as a variant of natural selection mechanism for human population.

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There is much discussion concerning natural selection efficiency in humans. Due to the fact that most factors limiting increase of human population have been overcome by scientific and technical progress the very existence of natural selection in humans is not obvious. Here a variant of such selection based on differential restriction of male fertility is suggested. It is known that human and domestic animals have a strong variation in efficiency of sperm production as compared to wild animals. Using flow cytofluorometric method we found wide variation in sperm chromatin organisation among different donors. More then 30% samples of sperm can be characterised as anomalous because they contain more then half of cells with disturbance in chromatin structure. The most part of this variation is due to the incapability of organism to protect the process of sperm production from harmful effects of diseases and other detrimental environmental factors. Comparison of these results with probability of pregnancy induced by in vitro fertilisation and following transfer of embrions to in vivo revealed a sharp decrease of chances for pregnancy for sperm samples where abnormal spermatozoa constituted a large part. This led me to think that it is a result of stopping of development before implantation on a stage where function of male genome becomes essential. One is tempted to speculate that such extreme sensitivity of male sex cells differentiation and mechanism for stopping of development due to distortions in sperm genome organisation may constitute the basis for natural selection in human population. Any hereditary changes that decrease protective possibilities of an organism could reduce male fertility and provoke differential reproduction. From the other side, disconnection of harmful hereditary changes and male fertility could promote their spreading in a population.

Plant performance in the rare Gentianella germanica in relation to population size, environmental and genetic (RAPD) variation.

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We studied the relationship between plant performance, population size, and environmental variation in the declining, short-lived plant G.germanica in 23 populations of different size (40 to 5000 flowering individuals) in nutrient-poor calcareous grasslands in NW Switzerland. To study whether differences between plants from different populations have a genetic basis, we grew 20 seed families from each of the populations in a common garden experiment. We used common garden plants from eleven populations to study genetic variation using RAPD (random amplified polymorphic DNA) profiles. Plants selected for the RAPD analysis represented similar areas in small and large populations.

Plants in small field populations produced a lower number of seeds per fruit and seeds per plant than plants in large populations. From 1993 to 1995 population size decreased in most populations and this decrease was larger in small populations than in large populations. Environmental variables accounted for some of the variation in population growth rate and plant performance. However, in stepwise multiple regressions effects of population size on plant performance were not confounded with effects of environmental parameters. Moreover, in the common garden survival and reproduction of plants originating from small populations was significantly lower than that of plants from large populations. There was a positive correlation between genetic variation (molecular variance) and population size. Genetic variation was also positively correlated with the number of seeds per plant in the field and the number of flowers per planted seed in the common garden experiment. We conclude that genetic deterioration is the most likely explanation for reduced plant fitness in small populations of G. germanica, though pollinator limitation may also have contributed to reduced fitness in the field. Our study supports the notion that genetic problems matter in plant conservation biology.

Queen mating frequency and offspring paternity in *Atta* leafcutter ants

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Multiple mating is likely to be very costly for ant queens and yet it occurs in 50% of the ant species that have been studied with genetic markers. In earlier studies we demonstrated unusually high levels of multiple mating by queens of the Panamanian leafcutter ant *Atta colombica* and found evidence that multiple mating may increase queen fitness because it allows them to obtain larger sperm stores. This was the first empirical evidence for ants that mating multiply may be adaptive for queens despite the likely severe costs. We now investigated the mating frequency of the Panamanian *Atta cephalotes* and *A. sexdens* using our previously developed *Atta* microsatellite DNA markers. Multiple mating by queens and multiple paternity of queens' offspring was demonstrated for both species. We discuss the patterns of queen mating frequency and offspring paternity across *Atta* leafcutter ants in relation to variation in male and queen body size and sperm content.

Causality relationships between changes in human personality and Toxoplasma gondii infection. Manipulation or an epidemiological risk factor?

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The manipulation hypothesis suggests that some parasites change the behaviour of their host to increase the probability of their transmission. In human an association between personality factors shift and latent asymptomatic toxoplasmosis has been demonstrated on the experimental set of 394 university students. Low superego strength (willingness to accept group moral standard) and affectothymia (warmheartedness) were most significantly increased in men and women, respectively (1, 2). The correlation between duration of toxoplasmosis and the intensity of superego strength decrease has been found for 164 male patients diagnosed with acute toxoplasmosis during past 13 years (2). This suggests that the changes in human personality were induced by the parasite (rather than that personality factors influence an acquisition rate of the infection). Similar data for female subjects, however, are missing.

In this study we measured antitoxoplasma antibody titres in 224 pregnant women whose personality profiles were measured with Cattell's questionnaire. The results showed an existence of a negative correlation between affectothymia and antibody titre for 60 toxoplasma -positive subjects (CFR IgG titre equal or higher than 1 : 8). As the level of an antibody titre decreases during latent toxoplasmosis, the observed relation indicates the existence of correlation between personality factor shift and duration of toxoplasmosis. This suggests that the personality factor shift developed after *T. gondii* infection and therefore could be caused by the manipulation activity of the parasite.

1) Folia Parasitologica 41: 122-126, 1994
2) Parasitology 113: 49-54, 1996

Founder effects, microsatellites and Lucilia

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Still, more than 40 years after their stipulation, some of the most discussed models of evolutionary change is Wright's shifting balance theory and Mayr's theory of allopatric speciation through founder effects.

There have been many theoretical models of how these changes are supposed to happen as well as laboratory work which supports the founder effect speciation theory.

I have chosen to study the effects of founder events on a model organism- the goldfly (*Lucilia illustris*). They breed on carrions which has a patchy distribution, and a single fertile female can give rise to several hundreds of offspring and could therfore give rise to a new population by herself. This life history feature of *Lucilia* species make them prone to go through founder events.

With the aid of microsatellites the genetic variation within and between fly populations is examined. The main question is if the populations have been founded by only a few indivduals.

Hidden Optimality of the Genetic Code

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Many evolutionary geneticists have sought to explain why the genetic code should take the precise form that it does. To a large extent these explanations fall into three categories: stochastic, deterministic (based on stereochemistry) and adaptive.

Work presented here considers the logical obstacles relating to the first two categories and explores an adaptive explanation based on "load minimisation". This is the idea that the genetic code is organised such that the net effect of mistranslation of codons and point mutations of DNA is minimised with respect to chemical differences in the resulting amino acids.

In particular this work considers the effect of weighting transition and transversion errors differently to give evidence that the genetic code is more highly adaptive than has previously been calculated.

Switching rules in ideal free distributions: differences in prey patches may have no influence on the distributions of predators using probabilistic switching rules.

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Predators choosing between two prey patches will base their choice on the reward they can reach in a given patch. If they know the future rewards, they should be distributed over the patches in a way that no predator can gain by switching to the alternative patch (ideal free distribution). In the simple case with a constant flow of new prey added to patches, input matching is reached, i.e. the ratio of predators and prey input is equal among patches.

However, under realistic circumstances, predators have to sample the patches to track fluctuations in the rewards they can expect. A switching rule that ensures regular sampling of both patches has been shown to drive the predator distribution away from input matching towards a uniform distribution (random choice of patch).

With more natural assumptions for the prey-predator system, namely a functional response type II for predator consumption and logistic growth of prey numbers, the resulting predator distribution changes more dramatically. Using mathematical models, I show that the use of two different probabilistic switching rules will result in a predator distribution that is almost always uniform, independent of prey densities: although the more profitable patch still attracts more predators, the differences in predator numbers between patches is less than 3 % of the total predator number over a range of prey growth parameters (intrinsic growth rate and carrying capacity) of between 1:10 and 10:1.

A comparison with individual-based simulations shows that in the majority of tested cases, these small differences predicted by the mathematical models vanish in the stochasticity of the simulations; the predator distribution is not significantly different from a uniform (i.e. 1:1) distribution between the two patches.

For observations and experiments under natural conditions, these results point at potentially severe difficulties in finding systematic deviations from a seemingly random predator distribution despite the presence of large differences in rewards that patches offer to predators.

Sperm dimensions in 20 mice taxa (Rodentia: Muridae): phylogeny and promiscuity?

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We examined the sperm dimensions (head, midpeace and principal piece lengths, head width) in 20 taxa belonging to rodent genera *Apodemus, Mus, Acomys*, *Lemniscomys, Arvicanthis* and *Mastomys.* Patterns of between-species variation in size of sperm-tail were examined and compared with the phylogeny of studied species. Evolutionary changes in the sperm length were used for the prediction of changes in mating systems, supposing that sperm-tail elongation should be associated with increasing sperm competition and promiscuity. The subgenera *Karstomys* and *Apodemus* share considerably longer sperm-tail than those found in the subgenus *Sylvaemus. A. sylvaticus* had longer sperm-tail than other studied species of the subgenus Sylvaemus. The aboriginal house mouse species (*Mus spretus, M. spicilegus, M. macedonicus*) had much shorter sperm than their commensal relatives (*M. musculus, M. domesticus*) and the laboratory mouse. *Acomys nesiotes*, *Lemniscomys barbarus*, and *Arvicanthis niloticus* showed similar values of sperm length as observed in the genus *Mus,* whereas sperm of domesticated *Mastomys coucha* differed considerably in both the head morphology and extreme length. The obvious tendency to longer sperm-tails in commensal species is discussed.

Evolution of reversible plastic responses: inducible defenses and environmental tolerance

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The selective advantage of reversible plastic responses is evaluated by a modeling approach within the concept of environmental tolerance (Gabriel and Lynch, 1992). This model predicts the selective advantage of irreversible plastic responses and is now expanded to include more flexible traits, e.g. temporal modifications of behavioral traits or inducible defenses that are rebuilt if no longer advantageous, like predator induced helmets in *Daphnia*.

Compared with an inflexible phenotype, the selective advantage of reversible plasticity in shifting the mode of the tolerance curve is large. The advantage increases exponentially both with the fitness loss of non-plastic phenotypes and with the difference t_s-t_r where t_s denotes the time span for which a shift is advantageous and t_r the sum of time needed for performing the shift forth and back. In many cases the gain in fitness is high enough to easily compensate all possible energetic costs of being plastic.

Plasticity in the breadth of adaptation is only weakly selected for if the change is irreversible. But for reversible plastic responses, a large breadth of adaptation becomes advantageous if the expected fitness reduction for inflexible genotypes is large. If t_r is not small compared to t_s then selection for plasticity in the breadth of adaptation can even be stronger than selection for shifting the mode of the tolerance curve.

Reversible plastic inducible defenses are expected to evolve under much less restrictive conditions than irreversible modifications, e.g. anytime the defense is advantageous for a short time span compared with the entire life span. Reversible plastic modifications are favored over constitutive defenses or irreversible plastic modifications particularly when the fitness loss without the defense is large.

The effect of life-history schedule, recruitment failures, and fishing mortality on the effective population size of pelagic fish

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This study investigates the effect of recruitment failures and variance in reproductive success on N_e in populations with type III survivorship curves. Special emphasis is put on determining the causes for the large differences in the genetic variability between populations of Pacific sardine and northern anchovy that inhabit the California Current System (CCS.)

The inbreeding effective population size is modelled using the coalescent approach introduced by Orive (Theor.Pop.Biol. 44:316-340; 1993) for stage-structured populations. This approach is extended to consider unequal parental contribution and temporal fluctuations in vital rates.

The analysis shows that moderate differences in life history schedule between closely related species can lead to substantial differences in N_e. Species with low generation overlap, such as anchovy, are likely to have higher N_e but are more sensitive to environmental fluctuations that can lead to increased variance in reproductive success and to recruitment failures. The ratio of N_e to census size is directly proportional to the total reproductive value but its sensitivity to environmental fluctuations is determined by the generation overlap.

The two most likely causes for the large difference in genetic variability between sardine and anchovy populations are life history differences and a recent arrival of the sardine population to the CCS (founder effect.) Although population size fluctuations in pelagic fish can be quite large, its impact on the level of genetic variability maintained is rather limited due to the buffering effect provided by the long lived stages. Moreover, although fisheries collapses can decrease to some extent genetic variability, they cannot be equated to population bottlenecks.

Evolutionarily stable dispersal rate in a metapopulation with extinctions and recolonisations

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We derive an analytic expression for the evolutionarily stable dispersal rate that formalises the balance between the effects of three factors: the cost of dispersal, the extinction rate and the coefficient of relatedness. This result allows us to study the effects of each factor and, more interestingly, to study the interactions between these factors. In particular we show that the evolutionarily stable dispersal rate is not always a decreasing function of the cost of dispersal. This counter intuitive result is discussed in the light of kin selection theory. We also present the results of numerical simulations in which the relatedness is not a fixed parameter but depends on dispersal and on the recolonisation process. In particular we study the effects of environmental factors (the cost of dispersal and the extinction rate) on the intensity of the parent-offspring conflict over the optimal dispersal rate. We discuss these results and show how both the viability of the metapopulation and the evolutionarily stable dispersal rate are affected by the environment and the life history traits of the species. In particular we present the effects of the mode of recolonisation (i.e. the probability of common origin of immigrants) on the evolution of dispersal.

Phylogeny of the genus *Chrysolina* (Chrysomelidae, Coleoptera) based in mitochondrial DNA sequences

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Chrysolina is a very speciose genus of leaf-beetles (Chrysomelidae) with large geographical distribution and marked oligophagy. Current taxomomy of the group based in classical characteristics such as morphology, karyology and trophism, divides the group into five main different lineages. We have started a project aiming to build up a molecular phylogenetic reconstruction using a DNA fragment of about 970 bp including the 3' end of cytochrome oxidase subunit I (COI), tRNAleu and majority of the sequence of cytochrome II gene (COII). Also, we are currently appraising the usefulness of the mitochondrial large ribosomal subunit and ITS nuclear sequences as relatively conserved and variable markers, respectively, for phylogenetic reconstruction. The aim of the work is to collect different molecular and non-molecular data sets with differential rates of evolution and to test the congruence or conflict among these, from which to deduce the evolution of *Chrysolina* beetles and its relation with oligophagy.

Fire history as a potential selective pressure acting on early stages of the life cycle of *Hyparrhenia diplandra* (Poaceae) in a West African savanna wild population.

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Tropical savanna ecosystems are subjected to annual fires and to unpredictable levels of water availability at the beginning of the rainy season. The impact of fire and drought was studied in *Hyparrhenia diplandra* (Poaceae), a common species of West African savannas (Ivory Coast). Fire and drought might be important selective pressures acting on post-dispersal seed survival and seedling survival, respectively. Diaspores of this species bear long hygroscopic awns. We have shown previously that (i) the mean germination time is significantly and positively correlated with mean awn length for each maternal plant and that (ii) there is a variation in the timing of germination among the seeds of all maternal plant and in all populations studied.

During the most recent flowering season, controlled crosses (self-, out-cross and open-pollination) were carried out on 30 plants in two patches differing in their fire history (fire-no fire). Effects of several morphological parameters of maternal plants (clump diameter, height, number of spikes) and diaspore awn length on diaspore dispersal distances were investigated. At the beginning of the rainy season, the germination time and the survivorship of all seeds were recorded in order to test whether morphological traits of the maternal plant, the origin of seeds (selfed, outcrossed and open-pollinated) and/or morphological traits of the diaspore (awn length) could influence the timing of seed germination and seedling survival.

Therefore, these data enable us to test for the influence of environmental factors (fire and drought) and mode of sexual reproduction on early stages of the life cycle of *Hyparrhenia diplandra*, on recruitment and consequently on maternal plant fitness.

Complex Evolution of a Microsatellite in the genus *Mus*.

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Compound microsatellites are loci in which two or more repetitive regions (e.g. $(CA)_n$ and $(GA)_n$) are found directly adjacent to one another. They comprise up to 15% of all microsatellites in some surveys. It has been proposed that compound microsatellites are derived from simple microsatellites by a two-step mutation process. First, a base substitution occurs within the repeat region and then the substitution is propagated by replication slippage, thereby creating a new repetitive region. Although this model is intuitively simple, there is little experimental evidence bearing on the issue of microsatellite origins.

In the course of screening mouse microsatellites for use in a behavioral ecology study, we discovered a large size difference between *Mus musculus* and *M. spicilegus* at a locus on Chromosome 1 (D1MIT29). Sequencing alleles from the two species revealed that this size difference was due to the fact that this locus was a simple locus in *M. musculus* and a compound locus in *M. spicilegus*. Sequencing of alleles of D1MIT29 in other *Mus* species demonstrated that, in fact, the simple locus was derived from a compound ancestor through a deletion event in the *M. musculus* lineage. Further, extensive variation between species in the single copy flanking region of the locus proved to be both phylogenetically informative and consistent with the tree derived from other types of genetic data. However, allele size was not informative, as distantly related species had alleles of the same size with very different sequence level structures. Finally, polarity in the distribution of variation at the locus suggest a non-random mutation mechanism operating in microsatellite regions. Comparative sequence-level data from other loci are necessary to determine to what extent our observations are consistent with the predominant mechanisms involved in microsatellite origination and evolution.

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To be or not to be a mutualist ?
Comparison of two ant species inhabiting the same plant species.

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Leonardoxa africana (Leguminosae : Caesalpinioidae) is an understorey tree of the coastal rainforests of Cameroon. It provides food (foliar nectar) and a nest (swollen, hollow internodes) for ants. Only two host-specific species of ants inhabit this tree (McKey 1984) The present study showed that their distributions were mutually exclusive: the formicine ant *Petalomyrmex phylax* occupied 2/3 of the trees sampled, while the myrmicine *Cataulacus mckeyi* occupied the remaining trees.

In order to know if the presence of ants was beneficial to the trees, we compared rates of damage on young leaves patrolled by ants and young leaves from which ants were excluded. We also made behavioural observations on the timing of ant activity and on the responses of ants to herbivores that they encountered.

Young leaves patrolled by *Petalomyrmex* suffered significantly less damage than those from which ants were excluded (2% versus 24%). In contrast, young leaves occupied by *Cataulacus* suffered from a far higher degree of herbivory (31%) than those patrolled by *Petalomyrmex*, a level not significantly different from that on ant-excluded leaves (46%). Behavioural observations help to explain the difference between the effects of the two ant species: *Petalomyrmex* workers patrolled young leaves constantly (day and night) and chased out or killed any phytophagous insects encountered. The patrolling activity of *Catalaucus* is only diurnal (rather well correlated with the activity of nectar production), and *Cataulacus* workers failed to consistently attack herbivores. These results indicate that *Petalomyrmex* is a mutualist and *Cataulacus* a parasite of *Leonardoxa africana*.

Counts of entire colonies revealed that *Petalomyrmex* allocated far more resources to colony maintenance (production of workers) versus colony reproduction (production of sexuals) than *Cataulacus*. Assuming that efficient protection is provided by numerous workers, it is not surprising to find this pattern of investment.

We discuss conditions under which a parasitic strategy is expected to be stable in plant ant systems, and we ask whether mutualisms may evolve from parasitic relationships.

Relationship of basal metabolic rate to colour types in males Pied Flycatcher *(Ficedula hypoleuca)* as a basis for maitenance of a stable population diversity

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The obtained results show that the basal metabolic rate (*BM*) in homeothermic animals is the fundamental scale of its energetic power and the indicator of the potential level of the daily work output. Increase in *BM* should increase in potential energy, potential productive energy, as far as should increase in work output and activity. Darker males of Pied Flycatcher are characterized by higher level of *BM*. Correlation between *BM* of male and their colour type (x, ranging from 1 - the darkest to 7 - the lightest) is: *BM*(mlO_2/bird*hour)=52.78-2.14*x, n=57
About 25 per cent difference between darkest and lightest colour types in males. The higher level of *BM* in males with darkest colour types makes them more adapted to lower ambient temperatures; optimum temperature for productive processes (reproduction included) is shifted by ca. 5^o-6^o C lower than in lighter colour types. To some extent, high *BM* of dark males may explain their tendency to breed earlier, predominance in northern part of the area and preference for polygamy, based on polyterritoriality. High *BM* of dark males may explain the trend of geographic variation of plumage colour in *F.h.hypoleuca*. It is this fact that accounts for the significant increase of the relative amount of the darkest males in the Northern parts of the area and higher in the mountains. We assumed that these males were potential competitors of dominants for preferred territories in the optimal habitat. The dark males have high *BM*, larger body mass and wing length. Dark males have better access to food and advantages in potential energy values over competitors. So they have better chances to maintain territories early in the season. Mean clutch size and reproductive success was higher in pairs with dark males than in pairs with lightest males. The most numerous intermediate form significantly differed from dark form in breeding dates.

Territoriality in birds: competition for better environment forms castes

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Territoriality is a complex property of animals and its development depends on many factors. One of the most considerable conditions is an adequate development of sensory systems that provides analysis of a territory and formation of territorial connections. A correct development of functional systems that provides formation of territorial connections in ontogeny requires the obligatory inflow adequate sensory information from environment. Natural species-specific behaviour of offsprings develops only in conditions of continuous receipt of this information. Then the territoriality in offsprings will form only at availability of "good" territory during critical periods of ontogeny. "Good territory" is the territory, which satisfies most requirements of the ecological niche of a particular animal. Population researches in two species of Passerines (Parus major and Ficedula hypoleuca) show that the high status of a male (high level of basal metabolism and some morphological parameters) determines its priority in the choice of breeding area in optimal habitats. This gives certain advantages for success surviving of breeding birds and their offsprings. Birds from the periphery of habitat are intent on nomadic manner of life. Thus offsprings of parents that have a better (adequate for ecological niche of species) territory imprint the territorial manner of live and for breeding will choice also a good territory. Offsprings grown up at a good territory have more chances to retain it because of better nurture and better knowing its characteristics. All the offsprings from the optimal habitat have morphological and physiological parameters higher than medial level while only part of them can inherit the good territory. All the other offsprings have to disperse. So at least two castes are formed inside the population: territorial and nomad. In such way a species fulfils all the tolerance range. The territoriality is the basic prerequisite for structuring of populations. It is the larger and better territory that may be the leading stimulus in the competitive interaction within populations.

The hypothesis on the reason for the basal metabolic rate to increase in the course of evolution in passerine birds

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Passerine birds prefer forest habitats and have basal metabolic rate *(BM)* which is 1.3-1.5 times higher than that in all other birds and mammals. I propose that the high *BM* of passerines is associated with their preference for forest habitats and migration potentialities. High flight speed are disadvantageous in these habitats. Aerodynamic theory show, that the power expenditure in flight depends on speed and on aerodynamic quality. On the other hand aerodynamic quality depends on head resistance. Head resistance in its turn depends on speed and on the external geometry of the bird. Hence it is possible to decrease speed by increasing head resistance. This way of setting the brake to reduce flight speed requires a lot of flight energy and shortens the duration of flight. Another way to reduce speed but, at the same time, to maintain a fairly long duration of flight is to change the type of flight. I allometric analysed both literary data and original data concerning the flight speed and aerodynamic characteristics of wing. My analysis shows that in Passeriformes, velocity is about 20% lower than in Non-Passerines, which agrees well with the inverted ratio of their of *BM* level. The regressions for aerodynamic characteristics of wing show that passerines do not change the morphological characteristics of the wing in order to decrease velocity. It is possible that the emergence of Passeriformes in evolutionary terms should be associated with their occupation of forest habitats. Thus it is possible to imagine that their adaptive radiation occurs as a result of this process. It can be said that in the range of smaller birds the energy potentials of passerine birds are significantly higher than those of nonpasserines and that the ecological niches most favorable for small forms are almost wholly occupied solely by passerines. Thus, the size range of 5-150 g for birds in forest habitats is almost exclusively occupied by passerines, as a consequence of their large energetic capability.

The origin of the homeothermy and boundaries of temperature resistance

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In this study were obtained new experimental facts: 1. The maximal ability of birds to change their thermal conductance was determined. 2. The character of maximal heat loss dependence on ambient temperature was determined. 3. The relationship between the maximal existence metabolism and the maximal ability to change nonevaporative heat loss was emphasised. 4. The relationship between the efficiency of metabolic energy transformation into mechanical form and the ability to change thermal conductance was established. 5. The relationship between basal metabolism and existence metabolism was established. 6. The evaporative water losses at different ambient temperature were determined both in Passeriformes and Non-Passeriformes. 7. The basal metabolic rate in homeothermic animals as fundamental scale of its energetic power and the indicator of the maximal level of the daily work output was shown. 8. The dependencies of thermal conductance on basal metabolism were determined both in Passeriformes and Non-Passeriformes.

The birds can change four times their heat loss at the same ambient temperature without intensifying evaporative heat loss. This ability is the basic characteristic of animal determining other important elements their energetics: the 3/4 mass exponent for basal metabolism, maximal existence metabolism (equal to 4 basal metabolism for all homeotherms), efficiency of transformation of metabolic energy into the mechanical form. The basal metabolic rate is the fundamental scale of animal energetic power and the indicator of the maximal level of the daily work output. Increase in basal metabolism should increase in potential energy, potential productive energy, as far as should increase in work output and activity. The relationship of *BM* to body mass with exponent 3/4 will indicate the ability of an animal (or a human) to perform work and allow us estimate its amount. The data obtained suggest the functional implication of the increase in BM in the course of evolution or in an particular animal.

Parasite host-range evolution: Experimental analyses of host-specific adaptation and host-switching

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We are interested in the microevolutionary processes surrounding host-switching by macroparasites. Our lab model is the zooparasitic nematode *Strongyloides ratti*. The approach adopts techniques and experimental designs commonly employed in studying ecological specialisation in other invertebrate taxa. Initial experiments attempted to select for altered host-specificity and the results and drawbacks of this work will be discussed. Inter-population differences in host utilisation success are also being examined alongside the role of "adaptive valleys" represented by vertebrate immune systems.

Keywords - parasites; specialisation; host-specificity; immunity

Geographical patterns of genetic variation in populations of *Dugesia polychroa*, a hermaphroditic planarian with sexual and parthenogenetic forms

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The planarian *Dugesia polychroa* (Platyhelminthes, Tricladida) is a free-living simultaneous hermaphrodite with diploid sexual and polyploid pseudogamous parthenogenetic forms. Parthenogens are distributed all over Europe, whereas sexuals are restricted to the south (Italy and Spain) where they often coexist with parthenogens to form mixed populations.

Using microsatellites, we have analyzed the genetic structure of pure parthenogenetic, pure sexual and coexisting sexual-parthenogenetic populations in Northern-Central Italy and Southern Germany. Results revealed a higher degree of genetic variation in populations situated south of the Alps whereas populations north of the Alps showed a low degree of genetic variation, probably due to recent recolonization after the last glaciation.

The coexisting sexual-parthenogenetic populations are of particular interest because the two biotypes can interbreed to form interbiotype-hybrids. Gene flow between the two biotypes has been detected in mixed populations by comparing combinations of microsatellite alleles between both reproductive modes.

The load of diploid male production and the queen mating frequency in the ant Formica truncorum

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Several hypotheses have been put forward in order to give an adaptive explanation for polyandry in eusocial Hymenoptera. The load hypothesis is based on their sex determination mechanism, and its peculiar side effects. Heterozygosity in the sex determination locus leads to femininization. Normally, hymenopteran males arise from unfertilised eggs but even those diploids that are homozygotes in the sex determination locus will develop into males. Diploid males are sterile, do not act as workers, and form part of the segregational load of the population. It has been proposed that the load by diploid male production would select for multiple mating by queens. This on one condition: double mating will be favoured over single mating only when the shape of the female fitness curve as function of diploid male production is concave. Should the fitness curve be convex, then single mating will be selected for.

This study attempted to quantify the load of diploid male production in different mating frequencies in the wood ant *Formica truncorum*. The load was measured in terms of reduction in the colony size, sexual production and colony growth rate. Frequency of diploid males within colonies was estimated by allozyme and microsatellite markers.The results indicate that the load of diploid male production depend on the queen mating frequency in a very intricate way, where sex ratio biasing by workers plays a crucial role.

A Polymorphic Duplicated Locus for PGI in Sheep´s Fescue, *Festuca ovina*

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Sheep´s fescue, *Festuca ovina*, has normally only one locus encoding the enzyme PGI. However, plants with a duplicated locus have been found at several localities in southern Sweden. Since gene duplication is one of the main mechanisms for genome evolution and diversification, this observation is worth further study.

PGI is highly variable at the main locus and two duplicated genes with the same electrophoretic mobility as two of the alleles at the primary locus have been found to map to a second, unlinked locus. A complex allele coding for both electrophoretic types has also been found to map to this locus. The alleles at the duplicated locus readily form heterodimers with all alleles at the main locus, thus giving rise to multibanded isozyme patterns when more than two different alleles are represented in a plant. The alleles at the second locus can be present in hemizygous or homozygous form.

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The attraction of mutualistic pollinators by receptive figs of *Ficus carica* L.

Marc Gibernau, Martine Hossaert-McKey and Finn Kjellberg.

Figs are urn-shaped inflorescences of *Ficus* species (*Moraceae*). The entrance of the fig, or ostiole, is tightly closed by bracts. Only specific insects (Hymenoptera: *Agaonidae*) can enter and pollinate flowers enclosed in figs. Moreover fig-wasps can only reproduce in their host figs by laying their eggs in the female flowers. This relationship is thus an obligatory mutualism. Almost each of the 750 *Ficus* species is pollinated by only a single fig-wasp species, this insect-plant relationship is moreover highly species-specific.

If odour has been admitted, since a long time, to be implied in the specific encounter of the two mutualistic partners. Surprisingly little is known about the exact role of odour in attracting fig-wasps.

Laboratory and field experiments were performed in order to test the role of volatile compounds emitted by receptive figs in pollinator attraction. Moreover gas-chromatography analyses were performed to identify the compounds present in different fig blends. Fig volatiles were compared to volatile compounds from other flower fragrances. Finally the importance of a blend (compound mixture) in odour evolution and specific insect attraction is developed.

Genetics of phenotypic plasticity: body pigmentation in Drosophila

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In *Drosophila melanogaster* as in many other insects, body pigmentation is sensitive to developmental temperature. As a rule, darker phenotypes are produced at low temperature and this is usually considered as an adaptive reaction in agreement with the thermal budget hypothesis. The isofemale line technique is a convenient way for genetic investigation of natural populations. Generally, ANOVA reveals a strong temperature x genotype interaction, but the genetics of plasticity is better analysed by looking at the shape of reaction norms. In this respect, polynomial adjustments provide a general, all purpose model. Various methods help to choose the polynomial degree. Different body segments exhibit different shapes of reaction norms, suggesting that pigmentation genes interfere with developmental genes. The genetic correlation between segments decreases when more distant segments are compared, showing an antero-posterior gradient. Geographic populations of the sibling species *D. melanogaster* and *D. simulans* have been compared. A convergence of the reaction norms of the two species has been observed in the same locality. Genetic differences between species or localities could be done by comparing either polynomial parameters or characteristic points of the norm. These data suggest that the shape of reaction norm can be modified by natural selection.

Gibert P., Moreteau B., Moreteau J. C. & J. R. David. 1996 - Growth temperature and adult pigmentation in two Drosophila sibling species : an adaptive convergence of reaction norms in sympatric populations ? Evolution 50: 2346-2353.

Reticulate evolution among species of the *Daphnia longispina* group

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In Europe, the most frequent species of the *Daphnia longispina* group (Crustacea, Phyllopoda) are *D. cucullata*, *D. galeata*, *D. hyalina* and *D. rosea*. Generally low morphological divergence and the prevalence of interspecific hybrids complicates the resolution of species. Even distantly related species are able to hybridize. Nevertheless, morphology and genetics are generally concordant, and mtDNA and nuclear introgression is assumed to be negligible among species. No stabilized introgressants have so far been reported from Europe.

Upon close examination, significant morphological divergence and ecological separation has been demonstrated for two species of the *D. longispina* group, *D. hyalina* and *D. rosea*. Yet, so far the species status has not received strong molecular support. Here, we present data from the analysis of rDNA ITS1 which show that the level of gene flow between allopatric populations from both species is much higher than previously assumed. Furthermore, size polymorphism of ITS1 suggests that gene flow among sympatric species is restricted. Generally, it has been reported that the level of intra-individual polymorphism of ITS is low. We find that the level of intra-individual sequence variation of ITS1 in specimen of previously assumed “pure” species is much higher. The rate of nuclear introgression might outweigh counteracting homogenization processes such as concerted evolution of multigene families. While intrachromosomal homogenization of tandemly repeated genes is assumed to occur rapidly, interchromosomal genetic exchanges during meiosis and recombination is assumed to occur at a very low rate. Daphnids reproduce by cyclic parthenogenesis. Predominant ameiotic parthenogenetic reproduction may favour a long persistance of intra-individual and intra-population sequence polymorphism.

Effective Drift!

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Silene dioica is a dioecious, diploid, perennial and bumblebee pollinated plant which disperses its seeds by gravity. It is a component of deciduous phases of primary and secondary successional communities in northern Europe. In Skeppsvik Archipelago, new islands are continuously formed by land uplift, providing new sites for *Silene* colonisation; later successional stages drive *Silene* to extinction on older islands. Earlier studies show that the degree of genetic differentiation among islands in the archipelago, and among patches within islands are increased by this perpetual colonisation and extinction dynamic. Differentiation within islands (spatial scale of a few meters) was twice as high as that among islands suggesting that even though genes are exchanged among islands, breeding units are small and local gene flow extremely limited. We have studied a tiny island where the entire *Silene* population of ca 500 individuals occupies 20x20m, and is in the early stages of establishment. Many patches consist of the first colonists and are spatially distinct, while other older patches have high densities, contain all life history stages, and are no longer spatially separated. Using F-statistics and coefficients of relatedness (r), we studied the changes in genetic constitution within and differentiation among patches as a function of age and spatial separation. We show that patches are founded by seeds from single females, and that patch differentiation remains high throughout population development. Breeding units are ca 0.5m^2 and effective population sizes about 5-10 individuals. The genetic constraints imposed by limited seed flow appear to be primarily responsible for restricted population size. Genetic drift is a strong force shaping the dynamics of these populations.

Statistical correlation of protein module with intron position

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Whether introns existed in ancestral genes of prokaryotes and eukaryotes or they were inserted later only into the genes of eukaryotes remains an unanswered question. Introns are often found between globular domains of proteins. More introns are located, however, within globular domains. A globular domain of proteins consists of compact modules which are contiguous segments of 10-40 amino acid residues. Modules are defined automatically using atomic coordinates of protein 3D structures and a computerized method. Introns of the genes encoding proteins were collected from various organisms. To investigate intron-module correlations extensively, we made a statistical analysis of the correlation of module boundaries of proteins and positions of introns of their genes. We found that the position of the introns had a significant correlation with module boundaries. The correlation cannot be explained by random insertion of introns, rather it suggests that (1) exons encoded modules even at an early stage of molecular evolution, and they were fused into genes encoding new functional proteins through the presence of introns, and (2) the primordial introns, which might be much shorter than the present-day introns, were apparently located at every module boundary in the ancestral genes of prokaryotes and eukaryotes, but a majority of such introns have been lost during the processes of evolution. Our result supports the view that (1) modules are vestiges of the original building blocks of proteins and shuffling units in protein evolution, and (2) the present and lost introns contributed as mediators of exon-shuffling.

Phylogeny of phytophagous beetles of the genus *Timarcha* (Chrysomelidae) based on molecular (COII) and life history traits

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We have studied the congruence among different data sets for phylogenetic inference in the chrysomelid *Timarcha*, a phytophagous flightless beetle mainly distributed in Palaeartic regions. Phylogeny reconstruction based on the entire cytochrome oxidase subunit II gene (COII) is currently complemented with data of the mitochondrial large ribosomal subunit and nuclear ribosomal ITS2 sequences. Life history traits such as trophism, karyology, distribution and morphology are used to test the molecular phylogenies obtained. DNA sequences from 20 Iberian species show the validity of COII as a molecular marker to infer phylogenies at the species level in this group. These data reinforce the existence of the so-called *Timarcha goettingensis* complex constituted by morphologically and karyologically indistinguishable taxa with disjunct geographical distribution which deserves further investigation.

Development of microsatellite primers and across-species transferability in the genus Limonium (Plumbaginaceae)

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In this work we present the development of a useful tool for the population analysis of species in genus *Limonium*. This is one of the 8 genus composing family Plumbaginaceae. Despite their cosmopolitan distribution, there are two well defined dispersal centers: the eastern Mediterranean and the Iran-Turkish region. In the Iberian Peninsula and Balearic Islands many endemic species can be found, with a high incidence of endangered taxa, due both to their ecological requirements and to increasing antropic pressure.

This genus presents two well defined groups of species according to their breeding systems. One is formed by poliploid species with apomictic reproduction whereas the other consists of diploid, sexually reproducing species with self-incompatibility mechanisms. Our goal is to study the genetic variation in populations of species from both groups for helping to design conservation measures and to compare the patterns of variation found between species from each breeding system.

Microsatellites are one of the most suitable tools currently available for this kind of study, due to their mendelian, codominant inheritance, high variability and abundance in eukaryotic genomes. We will present our progress in the identification and development of primers for SSRs on *L. narbonense*, and their usage with other 14 species form the genus.

The population structure of *Limonium dufourii*: a comparative analysis with RAPDs and AFLPs.

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A recently developed PCR-based fingerprinting technique called AFLP has been used for characterizing genetic diversity within and among populations of the endemic and endangered plant *L. dufourii* (Plumbaginaceae). This is a triploid species with apomictic reproduction of which only six populations persist in nature. We are analyzing the genetic variation, structure, and distribution in this species to help in devising a conservation strategy for it. Due to the small amount of material from each individual available for study, it has been necessary to resort to PCR based genetic markers. In this context, RAPDs and AFLPs appear among the most suitable techniques due to their relative low requirements on amount of DNA and no need for sequence information for their application.

Results of AFLP analysis are compared to a previous study of the same material using RAPDs. For fingerprinting methods, finding the appropriate techniques to analyse the data is particularly difficult because of their dominant inheritance. We show how these markers can be used in a population genetics framework, using currently available statistical techniques, even when Hardy-Weinberg equilibrium conditions do not hold.

The two methods provide similar conclusions regarding the relationships among individuals and populations. However, the combination of the new AFLP technique, coupled with the use of an automatic sequencer and fluorescence-based DNA detection system, provides a comparatively more reliable and efficient technology in terms of production of useful markers than other fingerprinting techniques, especially when dealing with conservation studies.

Biological regulation of the environment: what is this and does it really exist?

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The essential biochemical properties of living beings can be only maintained in a rather narrow interval of external conditions which can be roughly defined as conditions for liquid state of water. During the last three billion years Earth climate has "luckily" fitted into this narrow interval giving possibility for life to persist. Yet there exist a large number of abiotic processes (volcanic activity, increasing solar radiation etc.) that could in a rather short time have driven Earth climate to a state absolutely unfit for life (either complete glaciation as on Mars or complete evaporation of the oceans as on Venus with corresponding temperature and related changes). As it is not the case, this points to the existence of a force that would buffer any unfavourable for life changes in Earth environment. The only candidate for this role is the life itself - natural communities of biological species (natural biota).

Earth biota consumes solar radiation and thus processes a flux of information that by orders of magnitude exceeds all that can be processed by humankind. Organisation of metabolism processes makes it possible for biota to achieve a power several times exceeding that of modern humankind. This enables biota to impose a strong directed impact on the environment and regulate most important characteristics of Earth climate both on a local and global scale compensating any adverse changes of the environment. This has been shown for both marine (e.g. plankton) and land (e.g. forest) biological communities.

Biota appears as a number of independent structural units - ecosystems. Information coded in the genomes of species that form ecosystems determines ways of how such regulation of the environment is performed: each species knows what work it should do and not *any* species will do - a random set of species will not cope with such a complicated task. Such internal correlation of ecosystems is maintained by competitive interaction inside a "hyperpopulation" of ecosystems.

As any stable system, biota retains its stability only up to a certain threshold degree of perturbation. Substantially destroyed ecosystems (exploited forests, fields etc.) and domesticated species have lost their ability to regulate the environment.

We here discuss the pertinence of the above to the accepted view on evolution with adaptation to changing environment as the major driving force. The explanatory advantage of such understanding becomes doubtful if it is shown that biological species prevent global environment from any substantial changes, adaptation being of local nature and far less importance.

Community transformation of the environment: evidences and mechanisms of biotic regulation of the environment

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The discussion of the problems emphazised in the title is executed by the author predominatingly on an example of Scots pine (Pinus sylvestris L.) forests, widespread in the Eurasia.

1. A fundamental feature of Natural Communities is that during the restoration (and in the primary succession) they transform the environment, making it convenient for themselves (the various parameters of the environment vary 5-100 times).

After a disturbance the vegetational cover is restored to climax state.. A time of restoration in Scots pine forest spans about 150 years.

Both features and duration of the recovery process are identical in the communities of a given type in various parts of their area.

2. The climax (stationary) community support an ambient conditions invariant.

Climax community of a given type exists over a wide range of climatic and edaphic characteristics.

Natural stationary communities are able to compensate any external changes of environment both local and global ones, which confined within the limits of climatic and edaphic variations of characteristics at a territory of their natural distribution. Mechanisms of the disturbance compensation can be realized at study the recovery dynamics of communities.

Biological regulation of the environment: its role today

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Question to what extent the global biota controls the environment remains open. Biological regulation of the environment should be similar to the Le Chatellier principle in physics and chemistry: in natural ecosystems any environmental perturbation brings about biological processes aimed at its diminution. This prevents the environment from unfavourable for life changes. If biological regulation of the environment is substantial on a global scale, it can be best observed in areas with natural biota, where its complex mechanism is not yet broken due to injurious anthropogenic impacts. Ocean biota is much less perturbed by anthropogenic activities than land biota but as a possible important sink of carbon ocean biota has been ignored in most global change studies. We here use recent data on atmospheric O2 concentration change, the available estimates of major terms in global carbon budget (fossil fuel burning source and oceanic and atmospheric sinks of inorganic carbon) and different stoichiometric ratios for synthesis of organic matter by land and ocean biota. Closing global carbon and oxygen budgets we find a global oceanic biotic sink approximately equal to the global oceanic inorganic sink. We also independently find a land biotic source of about half that value which is in good agreement with data on land use and regrowth of temperate latitude forests.

Our results show that ocean biota captures the excessive carbon dioxide from the atmosphere in fairly large quantities and therefore diminishes the negative anthropogenic impact on the environment, while substantially perturbed land biota emits carbon and therefore contributes to the detrimental environmental changes. Thus the role of natural unperturbed biota in the global change processes becomes unequivocally clear: natural biota is a powerful mechanism capable of maintaining favourable for life environmental conditions.

Seasonal plasticity in two butterflies: The effect of seasonal state on reaction norms relating life history traits to photoperiod.

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The timing of life history events such as growth, maturation and reproduction is a crucial factor in the biology of any organism living in seasonal environments. Temperate insects typically use the photoperiod to determine the date and in this study we test predictions from optimality models of the general shape of reaction norms in response to photoperiod, focusing especially on development time.

The species in the study, *Lasiommata maera* and *Lopinga achine* are both univoltine in Sweden and spend the winter in diapause as half-grown larvae. From this follows that they have two distinct growth periods, before diapause in late summer and after diapause in spring. Hence, they face two timing problems, first to enter diapause in the autumn when photoperiods are becoming shorter as the season progresses, second to break diapause, grow and pupate in spring when photoperiods become progressively longer with season. To optimize both the timing of diapause in autumn and the timing of pupation in spring these species must have qualitatively different reaction norms during the two growth periods.

These predictions was tested in several controlled laboratory rearings and a state-dependent shift in the reaction norm relating development time to photoperiod was found in at least in one of the species. Thus, the same range of photoperiods was interpreted qualitatively different by the same individuals in autumn and spring, respectively. The effect on other life history traits such as growth rate, size at diapause and pupal weight was also consistent with predictions from optimality models. We conclude that these reaction norms are likely to be adaptations for optimizing individual time budgets in a seasonally varying environment.

Sexual selection and immunogenetic variation in the MHC

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The major histocompatibility complex (MHC) is an immunologically important and highly variable cluster of genes known to affect fitness in domesticated mammals and birds. Spur length of male pheasants living in the wild correlates with male viability, female mate choice, and offspring survival rate. We here show by genetic analyses that the MHC genotype is associated with variation in both male spur length and male viability. These are the first data on immunogenetic variation that directly support a "good genes" hypothesis by Hamilton and Zuk predicting that females discriminate among males on the basis of secondary sexual characters in order to pass on genes for disease resistance that improve fitness in their offspring.

Genetic and morphological systematic studies of the species Austropotamobius pallipes, (Decapoda: Astacidae).

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The white-clawed crayfish *Austropotamobius pallipes* is an indigenous and endangered species only recorded in Western Europe. According to Bott (1950, 1972), three subspecies are recognized in *A. pallipes* : *pallipes*, from Great Britain, Ireland, France, Switzerland and Corsica; *italicus*, from Italy, Dalmatia and Switzerland (Tessin); and *lusitanicus*, from the Iberian Peninsula. This recent classification of *A. pallipes* species is based exclusively on morphological, meristic characters and biogeography. However these characters are of limited value for identification purposes because they show considerable interpopulation variation. The possibility of misidentification of subspecies poses problems for management schemes including restocking purposes. Electrophoretic protein analysis revealed no genetic variation between these subspecies. We propose a method for unequivocal identification of these subspecies based on analysis of mtDNA by RFLP. UPGMA analysis from nucleotide distance between haplotypes revealed two clusters, *A. p. italicus-A. p. lusitanicus* and *A. p. pallipes*. However, the high levels of nucleotide divergence (8 - 13 %) revealed between haplotypes characterizing the three subspecies show the important role of the biogeographic barriers formed by the Pyrenees and Alps in the lack of gene flow allowing divergence to accumulate. This study confirms the suitability of mtDNA for phylogeographic studies allowing inference in the biogeography, history and evolution of the populations and taxa. In conservation purpose, the strong genetic divergence between *A. pallipes* subspecies requires that the mixing populations should be avoided in the case of restocking purposes.

Female co-operation in Allodapine bees seen from a class structured perspective: evolution of sex ratios and colony sizes

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To understand the important interactions during the origin of eusociality it is often worth studying more primitively social taxa. The allodapine bees offer us this opportunity and the presence of a number of traits makes them an interesting subject. Of specific interest are the positive interactions between female relatives observed in these bees. Groups of sisters and nieces construct nests together and in a number of species it has been shown that the per capita reproduction of bigger groups is higher than those of small ones. It has been proposed that this relationship between group size and reproductive output has shaped a number of traits in these societies.

Firstly, the positive interactions between sisters have been argued to bias the sex ratios towards females. This is the flip side of local resource competition (LRC) between sisters that leads to male biased sex ratios. The female bias, can in turn predispose the taxon to evolve to complete eusociality, given that the bias is in equilibrium from the parents point of view. However, verbal arguments have been raised suggesting that the flip side of LRC may not lead to stable female biased sex ratios.

Secondly, such positive group associations should naturally select for bigger group sizes and will therefore select for individuals who form coalitions with relatives more regularly.

As yet, no formal models have been developed to support these verbal arguments. Here I use Taylor's method of thinking of gene frequency changes in class structured populations to analyse these problems. Models suggest that sex ratio trends may in fact not be in equilibrium. Several arguments are raised to try and explain the stability observed in nature. The most interesting of these is the role policing may play. Policing at the level of individuals may stabilise sex ratio trends at the higher hierarchical level, namely the class of colonies of a certain size.

Population phylogeny of the gecko *Tarentola delalandii* on Tenerife, Canary Islands

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The within-island evolution of the Tenerife gecko is studied using mitochondrial DNA sequence data from the cytochrome b gene. The molecular phylogeny is tested against alternative historical hypothesis by employing matrix correspondance tests. The results are discussed in relation to geological data and earlier studies on geographic variation in morphology.

23 years of evolution of adaptive genes in the mosquito *Culex pipiens*: allele replacement and changing environment

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How adaptive genes evolve in natural populations ? Twenty tree years of evolution of insecticide resistance genes in the mosquito *Culex pipiens* from Montpellier are analysed, with the aim of answering to the following :

1) is there a pleiotropic effect on fitness associated with resistance genes in natural populations ?

2) Does evolution proceed through allele replacement of resistance alleles (e.g. less costly alleles replacing more costly ones) or through selection of modifiers (reducing the cost) ?

3) How environmental changes (insecticide replacement, variation in the treated area) affect the evolution of resistance genes ?

METHANOGENIC BACTERIA AND ANAEROBIC PROTISTS IN THE GUTS - EVOLUTIONARY ASPECTS*)

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It has been assumed that the feeding habits of animals predispose the variety of intestinal differentiations and the composition of the intestinal microbiota. Consequently, the presence of methanogenic bacteria in the gut of herbivorous animals had been attributed to the existence of anaerobic habitats and the availability of carbon dioxide and hydrogen that originate from the fermentative, microbial digestion of plant-based diets.

More than 160 species of arthropods and 253 species of vertebrates were screened for methane emissions in order to test the validity of these assumptions. The results of these screens, however, did not reveal a consistent positive correlation between methane production and vegetarian feeding habits: there are herbivorous animals that lack intestinal methanogens and carnivorous species that can host methanogens (Hackstein & Stumm 1994; Hackstein and van Alen 1996). The taxonomic position, and hence the evolutionary descent, of the hosts appeared to be crucial for both the presence of methanogenic bacteria and the evolution of the various types of "fermentative" intestinal differentiations. Also the presence of symbiotic intestinal protists seemed to be governed by the same constraints.

Hackstein, J.H.P. & Stumm, C.K. (1994) *Proc. Natl. Acad. Sci. USA.* 91, 5441-5445,
Hackstein, J.H.P. & van Alen, T.A. (1996) *Evolution* 50, 559-572

*) Dedicated to the memory of Rudolf A. Prins

Intron evolution in insect hemoglobin genes

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The aquatic larvae of chironomid midges contain a number of monomeric and homodimeric single domain Hbs, which are essential for the survival of the animals in an oxygen poor environment. These Hb protein variants are encoded by an exceptionally large multigene family (>40 genes). In contrast to the globin genes of many other organisms the vast majority of chironomid Hb genes are intronless. However, a few Hb genes contain "central" introns in some species, while the orthologous genes in related species are free of introns. A survey for introns in the Hb genes 2b, 9 and 7A in 15 different species of four distantly related species groups showed the following results: the camptochironomids (C. tentans and C. pallidivittatus) have no introns in any of the three Hb genes; the Australasian species (C. jacksonii, C. duplex, C. oppositus, C. zealandicus) also do not have introns in the Hb2b, 9 and 7A genes. The C. melanotus species group (C. melanotus, C. cingulatus and C. annularius) has an Hb2b gene which contains a short "central" intron in the position between codons 14 and 15 of the E-helix. The C. thummi species group (C. thummi, C. piger, C. halophilus, C. pseudothummi) contains short central introns in all three Hb genes (2b, 9 and 7A) at position 9/1 of the E-helix. The sequences of these thummi-group introns show a higher degree of sequence identity in the three paralogous genes than the coding sequences themselves. This indicates a concerted evolution of intron sequences, possibly by gene conversion. The thummi-group introns are not related to the melanotus-type intron. It seems improbable that these sporadically occurring introns represent ancient central introns, which have already been present before the expansion of the chironomid Hb gene family. The most parsimonious explanation for our data is given by two independent integrations of intron sequences into chironomid Hb genes: one which happened in the ancestor of the melanotus species group and the other in the progenitor of the thummi species group. Within this thummi ancestor, the inserted intron may have spread to neighbouring Hb genes. This interpretation of our data is compatible with the "introns-late“ hypothesis. As expected for introns which insert more or less randomly into genes late during evolution, we have now found three more, unrelated introns at different positions in three new Hb genes isolated from the chironomid species C. tentans and G. barbipes.

The ancestry of modern humans: inferences on gene trees for β-globin sequences

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In the first major study of allelic sequence variation for an autosomal nuclear DNA locus we determined 349 3-kb β-globin sequences from nine populations. A unique gene tree was constructed from 326 sequences and analysed by new maximum-likelihood methods for estimating the mutation parameter θ ($=4N_e\mu$) and conditional time-depth assuming a coalescent model. The level of diversity observed was consistent with an effective population size, N_e, of 10,000 approximately. No evidence was found for exponential population expansion. We found that allelic β-globin variation coalesced to a single shared ancestral haplotype over a time-scale of at least 800,000 years. This particular haplotype was only found in African samples. In gene trees for all populations sampled are three major lineages, including one that appears to be rare in Africa but widely distributed in Asia. The two oldest alleles in this lineage were found exclusively in Asian samples. A globally widespread distribution of a fourth lineage was found at frequencies of 1-5%. Patterns of β-globin diversity suggest extensive worldwide late Pleistocene gene flow. Characteristically Asian diversity was estimated to be older than 200,000 years. We have inferred from these results that the genetic ancestry of modern humans in earlier archaic populations includes both African and Asian lineages.

Spatial autocorrelation analysis and the estimation of gene dispersal within a continuous population: investigation by numerical simulations

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The analysis of fine scale genetic structure is an important topic both in theories of evolutionary biology and population genetics and, in practice, to define optimal sampling strategies for germplasm conservation purposes. The pattern of spatial genetic differentiation reflects past evolutionary processes, involving natural selection, demography (founder effect) and, in particular, gene flow.

Within continuous populations, spatial autocorrelation analysis (e.g. Moran's I statistics, join-counts statistics) have been successfully used to detect fine scale genetic structure and, in a few cases, to give rough estimates of the level of gene dispersal. However, those statistics have not been related to theoretical models of continuous populations like those developped by G. Malécot or T. Maruyama. The latters established relationships between the coefficient of kinship according to distance and gene flow parameters (variance of gene dispersal distances, incoming migration rate of genes).

Using numerical simulations, we show that the Fr(r) function proposed by H. Van Dijk and which amounts to a generalisation of Wright's fixation index F for any distance r separating alleles, provides an estimate of the mean conditional kinship coefficient in population submitted solely to restricted gene dispersal. Therefore, correlograms constructed with this function can be used to infer the level of gene dispersal within continuous populations. Relationships between this function and Moran's I statistics have also been derived.

Splicing patterns of M- and O-type *P* elements

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Two subfamilies of *P* transposons (M-type and O-type) coexist in the genome of *D. bifasciata*, a member of the *D. obscura* species group. M-type elements are similar to the *P* elements of *D. melanogaster* (the species where *P* elements have been discovered), but even more closely related to *P* elements of *Scaptomyza pallida* and probably have been derived from this genus through horizontal transfer. Within the *obscura* group they are found in the sibling species *D. bifasciata* and *D. imaii* and in their remote relative *D. helvetica*. O-type elements occur in *D. bifasciata*, *D. imaii*, and in *S. pallida*. They are supposed to have invaded the *D. bifasciata* lineage from *S. pallida* in a second, more recent horizontal transfer. Both M- and O-type elements have the coding capacity for two proteins: transposase (germline) and repressor of transposition (somatic tissue). In *D. melanogaster*, it has been shown that restriction of transposase production to the germline is due to alternative splicing of the third intron. We applied RT-PCR to find out if both *P* element types are transcribed in the various species and if repressor and/or transposase mRNA are produced. Moreover we investigated if the same tissue specific splicing patterns are found as in *D. melanogaster*. The results suggest that M-type elements are mobile in *D. helvetica* which harbours only this *P* element type. In both species with two *P* element types (*D. bifasciata* and *S. pallida*) the older one (=M-type) is obviously inactivated whereas the O-type seems to be transpositionally active. Moreover, we discovered two new splicing variants of intron 3´coding for repressor- or transposase-like proteins respectively. The new splicing sites are highly conserved among all *P* element types investigated so far. We could show that the production of the various mRNA variants is regulated in a tissue-, type- and host-specific manner. The proteins encoded by these mRNAs could be involved in the fine tuning of transpositional regulation.

Early avian evolution: molecular dating of the divergence between paleognathous and neognathous birds

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The deepest divergence among extant bird orders is generally acknowledged to be that between paleognathous and neognathous birds. We have sequenced and analyseded the complete mitochondrial (mt) genomes of two paleognathous birds, the ostrich (Struthio camelus) and the rhea (Rhea americana). The only complete mt genome of a neognathous bird, currently available, is that of the chicken. Using external mammalian and reptilian references, we dated the divergence between neognathous and paleognathous birds at 85-90 million years before present time (MYBP). This is surprisingly recent and somewhat lower than expected (Cooper and Penny 1997).

Therefore, a parallell study was done on the complete cytochrome b gene, including seven bird orders. The analysis identified the passeriform birds as the most basal avian branch. Thus, the primary divergence among extant bird orders may not be that between paleognathous and neognathous birds, but between Passeriformes and the remaining orders. These findings challenge the palegnathous/neognathous dogma.

CROSS-SPECIES-AMPLIFICATION OF *DROSOPHILA* MICROSATELLITES-A DIFFERENT MUTATION PATTERN IN *D. MELANOGASTER*

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15 Microsatellite loci isolated from *Drosophila melanogaster* were used to amplify orthologous microsatellite loci in *Drosophila simulans*, a sibling species of *D. melanogaster*. Both species originated in Africa and colonized the rest of the world only about 10,000 years ago.

As expected *D. melanogaster* and *D. simulans* are more variable in African populations. Variances of all loci amplifying in both species were on average 37% higher in *D. simulans* and 26% higher in *D. melanogaster*. Similarly, gene diversities were also higher in Africa, averaging 26% in *D. simulans* and 17% in *D. melanogaster*.

To test whether a variation in mutational behavior occurs we compared variances in repeat number within and between species. For within species analysis we compared an African and non-African group of each species. If mutational behavior between these groups is constant then the variances of different loci should be correlated. We plotted the observed variance in the African population against the observed variance in non-African populations and found a highly significant correlation in both species ($P > 0.0005$). Therefore, the mutational behavior of microsatellites seems to be fairly constant within a species.

Comparisons of *D. melanogaster* and *D. simulans* did not yield a significant correlation ($P<0.5$). This can be best explained by different mutational behavior of microsatellite loci in *D. melanogaster* and *D. simulans*. Those differences can be attributed either to differences in mutation rates or different constraints acting on allele size. Our results indicate that microsatellite based distances for cross species analysis may be handled with care.

Avian nucleotide substitution patterns: implications for phylogeny reconstruction

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The reconstruction of phylogenies has increased dramatically since the advent of modern molecular techniques. The increased use of phylogenetic information prompts for a need to assess the accuracy of different methods for inferring phylogenies using molecular data, such as maximum parsimony (MP), maximum likelihood (ML), and distance methods accompanied by the neighbor-joining (NJ) algorithm. ML and distance methods rely on detailed models of nucleotide substitution, whereas MP avoids the use of particular models for the benefit of generality. In birds the patterns of *cyt-b* nucletide substitution is different from the models published so far. Our question is simple; given an unknown model, is it possible to obtain reliable results using approximate, but wrong, models to estimate phylogenies, or is a more model-free method more reliable?

We simulated a large number of data sets of 10 species starting from a known avian sequence and using the substitution patterns found in birds, and subsequently applied all methods to infer the phylogenies and branch-lengths. The inferred trees were then compared to the true one.

In general, when all information is used most methods produced acceptable results (true tree found in 90 % of the data sets), with MP being superior to distance and ML methods. However, the estimation of branch-lenghts was in general poor; some methods consistently overestimated branch-lengths, while others consistently underestimated branch-lengths. Excluding third positions resulted in a drastic drop in performance - although MP methods were again superior to all other methods, they found the true tree in only 20 % of the cases. Thus, weighting according to position is not recommendable. In general, regardless of method phylogenies at lower taxonomic levels (lower amount of variation) was easier to infer than phylogenies at higher level.

Genetics and taxonomy of Nile perch, *Lates niloticus*, introduced to Lake Victoria, East Africa

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Although the introduction of Nile perch to Lake Victoria has received intense global attention, especially in relation to the extinction of many endemic cichlid species, fundamental information on its taxonomy and population genetics is lacking. Most importantly, the introduced fish originated from two lakes (Lakes Albert and Turkana) containing three *Lates* species, and it has never been entirely clear which of these became established in Lake Victoria, or indeed whether the Lake Victoria population is derived from hybridisation between species. In addition, genetic drift caused by the relatively small founder population (approx. 400) and the delayed population increase in Lake Victoria, as well as selection pressures in the new environment may have resulted in substantial genetic changes.

Allozyme electrophoresis was used to assess taxonomic affinities of Lake Victoria *Lates* to possible source populations. Results suggested strongly that the introduced fish are indeed *L. niloticus*, introduced from Lake Albert (Uganda, Zaire). In contrast, none of the other species appears to have become established in Lake Victoria.

There were indications for a founder effect during and after the introduction of Nile perch, as allelic diversity was lower in the introduced populations. In addition, the Lake Victoria fish and Nile perch introduced to other lakes (Lakes Kyoga and Nabugabo) were genetically differentiated, suggesting random genetic drift in the founder populations. The reduction in genetic variability may affect the adaptability and thus the persistence of the introduced population in the rapidly changing environment of Lake Victoria, and may therefore have implications for the management of the fishery as well as for the conservation of endangered cichlids.

Fitness of hybrids between oilseed rape and weedy *Brassica campestris*: possibilities for introgression of transgenes from crops to wild species?

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It is known that genes are sometimes exchanged between crops and non-cultivated related species via spontaneous introgression. With the use of genetically engineered crops, the transgenes may likewise be transferred to other species. The probability of this is mainly determined by the sexual compatibility of the two species, and on the fitness of the first and advanced generation hybrids.

In a series of crossing experiments we have addressed the fitness of hybrids between oilseed rape (*B. napus*) and weedy Danish *B. campestris* (=*B. rapa*). In the first generation, reciprocal crossings were made between three *B. napus* cultivars and three *B. campestris* populations. The hybrids were found to have a lower fitness than their parents for some life-stages and a higher fitness for others. A combined estimate revealed that the F_1 hybrids may sometimes be as fit, or more fit than *B. campestris*. In the second generation crossings, two *B. napus* varieties, two *B. campestris* populations, and F_1 hybrids between these were intermated to obtain F_2 and reciprocal backcrosses. Here, both the backcross and the F_2 plants were depressed in fitness relative to pure *B. campestris* and *B. napus* plants for most life-stages and for the overall estimate. A large variation was detected in the fitness of the second generation hybrids, suggesting that some hybrids may still be among the surviving and reproducing plants in the field. Also, as parental *B. campestris* populations, *B. napus* varieties, and families of the two species differed with respect to the fitness of their hybrid offspring in the two crossing generations, the likelihood of introgression of transgenes may vary dependent on the crop variety used and on the characteristics of the local populations of the weeds.

Reproductive conflict in ant societies

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Wherever animals live together in social groups, conflicts arise about the partitioning of reproduction among group members. According to models on reproductive skew, whether and how strongly reproductive success differs between individuals depends on ecological and genetic factors, such as the average fitness of dispersers, genetic relatedness, the number of individuals, and the benefits from helping.

In the colonies of social Hymenoptera, interests of workers and queens and among workers may diverge about the origin of males, and among queens about who produces how many male and female progeny. In the ant genus *Leptothorax*, these conflicts may lead to aggressive interactions among nestmates, which finally result in the formation of social and reproductive hierarchies. Fighting mostly consists of ritualized antennation bouts and stilting dominance postures, but eventually may escalate to openly aggressive biting, pulling with the mandibles on the opponent's antennae or legs, and using the sting to smear gland secretions onto the opponent's cuticle.

As workers in monogynous colonies are on average more closely related than queens in multiply-queened societies, and the reproductive success of dispersing workers is much smaller than that of dispersing queens, one might expect that hierarchies among workers are established by less violent interactions than those among queens and that workers tolerate higher reproductive skew than queens. Antagonism among nestmate workers indeed appears generally less fierce than among queens. Nevertheless, whereas in queen hierarchies typically only one high ranking individual becomes fully fertile, in worker hierarchies a larger number of workers lay unfertilized eggs. This might reflect the different reproductive potential of the two female castes or the higher number of interacting individuals in worker hierarchies.

Pleistocene effects on the distribution of genomes revealed by different DNA markers

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The genetic effects of pleistocene ice ages can be illuminated by a combination of deduction from paleoenvironmental information and induction from the genetic structure of populations and species. (1) Recent paleoclimate information indicates rapid global reversals and changes in ranges of species which would involve elimination, with subsequent spreading from the refugial edge. Leading edge colonisation during a rapid expansion would be leptokurtic and lead to homozygosity and spatial assortment of genomes. In Europe and North America, ice age contractions were into southern refugia, which would promote genome reorganisation. Boreal, temperate, desert and tropical species ranges would be affected differently. (2) The present day genetic structure of species shows frequent geographic subdivision, with parapatric genomes, hybrid zones and suture zones. A survey of recent DNA phylogeographic information supports and extends earlier work. (3) It also shows that mtDNA and cpDNA markers are used predominantly, and yet others recommend themselves, e.g. ITS rDNA, anonymous nuclear, introns, MHC and microsatellites. Their attributes will be discussed. (4) The grasshopper *Chorthippus parallelus* is used to illustrate such data and processes. Its range in Europe is divided on DNA sequences into 5 parapatric races, with southern genomes showing greater haplotype diversity - probably due to southern mountain blocks acting as refugia and northern expansion reducing diversity. (5) Comparison with other recent studies shows a concordance of such phylogeographic data over pleistocene time scales. (6) Repeated contraction and expansion would accumulate genome differences and adaptations, protected from mixing by hybrid zones, and such a composite mode of divergence and speciation could apply to many organisms.

IMPACT OF DRIFT AND DEMOGRAPHY ON GENE FREQUENCY CHANGES IN THE SAGUENAY POPULATION OF NORTH EAST QUEBEC.

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We present results based on the known demographic history of an human population: the Saguenay population. This population has been created through a founder effect 300 years ago. We use computer simulations on known genealogical paths to measure the extent of genetic drift due to mendelian segregation. The extent of gene frequencies changes due to demographic parameters were obtained by calculation of the genetic contribution of founders to the contemporary population. In NE Québec (Saguenay Region) some inherited disorders can be found at a carrier frequency of 1/25. These disorders were introduced in the population before 1700; the results of molecular studies strongly suggest that a single founder was responsible for any particular disease. Since around 5000 individuals settled in Quebec before 1700, the present day carrier rate of up to 5% has to be accounted for by demographic parameters and by genetic drift. Our approach enables us to discriminate between the effect of drift and demography and also to test weather the "single founder" hypothesis is valid. We will also compare the fate of a lethal recessive gene with a neutral one.

Life history variation in *Bosmina coregoni* relative to seasonally changing selective factors

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We studied clonal succession of *Bosmina coregoni* during the growth season in Lake Pyhäjärvi (SW Finland). Samples of clones were isolated from the field population and acclimated to laboratory conditions. Clonal succession should be seen as different responses of experimental animals. Sampling dates were chosen to represent critical periods for population structure; spring maximum, summer minimum and autumn maximum. Life table experiments were run in laboratory to evaluate dependence of life history traits on the amount of food.

Clone sets isolated from early summer population contained significantly larger animals than sets that were isolated from the middle summer and autumn populations. Although body size changed, neither reproductive instar nor mean clutch size changed during summer. Food level affected life history traits; age at the maturity, for instance, was negatively correlated with food level. The largest clutches were produced at intermediate food levels. Our results indicate that changes in size distribution, size at maturity and offspring size in natural *Bosmina* population were due to changes in clonal composition. These seasonal changes were probably caused by the selective predator of vendace, although food composition also changed during the summer.

Compensatory Mutations and the Evolution of RNA

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There are many examples of RNA molecules where the secondary structure has been strongly conserved during evolution, but the base sequence is much less conserved. A model of compensatory neutral mutations is used here to describe the evolution of the base sequence in RNA helices. There are two sites (i.e. the two sides of a pair) with four possible bases at each site. Watson Crick base pairs (AU, CG, GC, and UA) are each assigned a fitness 1, whilst all other pairs are treated as mismatches and assigned fitness 1-s. A population of N diploid individuals is considered with a mutation rate of u per base.

Using a diffusion model the stationary distribution for the frequency of any of the four matching pairs is calculated. The key parameter combination controlling the distribution is Nu^2/s. When this combination is small, the population typically consists of almost entirely one of the four types of matching pairs, but occasionally makes shifts between the four possible states. The mean rate at which these shifts occur is calculated here. The effect of recombination between the two sides of the pair is to decrease the probability density at intermediate frequencies, and to increase the weight at the extremes. The rate of transition between the four states is slowed by recombination (as originally shown by Kimura in a two allele model with irreversible mutation). A very small recombination rate is sufficient to dramatically increase the mean time between transitions.

This analytical theory describing a single RNA base pair will be related to observations on the frequency of compensatory mutations in RNA sequence databases. It will also be used to interpret simulations of the evolution of complete RNA sequences on fitness landscapes which are functions of secondary structure. An understanding of the rate of evolution in RNA helices can be used to develop more accurate methods of construction of phylogenies from sequence data.

Modelling coevolution in multispecies communities

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We introduce a model to describe the structure of food webs and the dynamics of ecological communities on an evolutionary timescale. Species are defined as sets of characteristic features, and these features are used to determine the position of links between species in the web. A simple rule is used to transfer resources from the external environment through the food chain to each of the species, and to determine mean population sizes. Species whose population is less than a certain minimum value are assumed to become extinct. A time step in the model represents a speciation event. A new species is added with features similar to those of one of the existing species. A new food web structure is calculated. The new species may either (i) immediately become extinct because it is poorly adapted, (ii) add to the web in a stable manner, (iii) cause the web to become unstable, so that one or more other species become extinct.

We compare several properties of the webs with measured data on real food webs. These properties include the total number of species at basal, intermediate and top trophic levels, the number of links per species, the distribution of lengths of food chains, and the degree of similarity between species in the web (as measured by the proportion of features which they share). We also consider the dynamics of the web by measuring the changes in the number of species as a function of time. For some parameter values there are very large fluctuations in the number of species when many species simultaneously become extinct. We relate this to observed extinction events in the fossil record, and to the theory of self-organized criticality.

Hide or fight? The competitive evolution of concealment and encapsulation in host-parasitoid associations

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I employ a mathematical model integrating the population and co-adaptive dynamics of an insect host and its specialist parasitoid wasp to investigate the competitive evolution of two forms of host resistance: concealment (or camouflage) from adult parasitoid location and encapsulation of developing juvenile parasitoids. Evolution of the host alone results in no differences between the equilibrium frequencies of the two forms of resistance. However, when the parasitoid is allowed to co-evolve with the host the frequency of hosts concealing themselves always exceeds the frequency of hosts capable of encapsulating juvenile parasitoids. This result holds when comparing each form of resistance evolving alone or in tandem. The mechanism driving the difference between the two forms of resistance is that parasitoids lose more reproductive effort when the host encapsulates as compared to when it is concealed or camouflaged. The main testable prediction of this study is that concealment is most likely to dominate encapsulation when hosts are relatively common and/or parasitism rates relatively low.

Egg limitation: a phylogenetic constraint for the evolution of sociality in carpenter bees?

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The carpenter bees (which include the large Xylocopini and the small Allodapini), have many pre-adaptations to social behaviour, such as overlap of generations and feeding of nestmates by trophallaxis.A frequently raised question is why a morphologically based caste system has not evolved in this group of bees.

Here, the hypothesis is raised that the production of giant eggs, common throughout the taxon, and especially in the mass provisioning Xylocopini, constrains the evolution of sociality. Giant eggs potentially limit the egg laying rate of females. In that case, helping by subordinate females might not increase the egg laying rate by the dominant female, and therefore may not lead to sufficient payoffs for helping behaviour to evolve. Thus, egg limitation may be a phylogenetic constraint to the evolution of eusociality in this group.

Some allodapine species show incipient stages of sociality. In such nests, there is usually one dominant female and several, morphologically indistinguishable subordinates. These bees feed their brood progressively, which allows a decoupling of egg laying and foraging over time. In some species eggs are stock piled over winter, and large numbers of eggs may be present in the nests when foraging starts. In social nests, this will increase pay-offs of helping behaviour. The causal relation between egg stock piling and sociality is supported by two findings: 1) Egg stock piling occurs only in species that are largely semi-social during the onset of the flight season; 2) Dominant females in large nests, that contain many potential helpers, start laying eggs earlier during winter than dominant females in small nests.

Therefore, stock piling may enhance social nesting when the egg laying rate of the dominant female is limited. In addition, these findings support the hypothesis that the large eggs are a constraint to the evolution of sociality in mass provisioning Xylocopini.

Unraveling genetic patterns of postmating reproductive isolation -- Haldane's Rule or Haldane's Coincidence?

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Evaluating models proposed to explain Haldane's Rule (the observation that the heterogametic sex is preferentially affected in species hybridizations) requires experimental evidence that is, at best, difficult to obtain. This is primarily true because unraveling Haldane's Rule requires dissecting the genetic patterns of species incompatibilities, that, by their very nature, are traits that do not yield easily to genetic analyses. Most genetic studies have implicated the *X* chromosome as being principally responsible for causing hybrid sterility, and to a lesser extent, hybrid inviability in crosses between different species. Both this large effect of the *X* chromosome and Haldane's Rule have been explained by a model (Charlesworth, Coyne, and Barton, 1987) that predicts that the *X* chromosome will evolve more rapidly than the autosomes because of increased opportunity for natural selection to act on sex-linked traits in hemizygous individuals, thus leading to a greater number of incompatibility genes in the heterogametic sex than in the homogametic sex in species crosses. More recently this model has been challenged by a more general model (Turelli and Orr, 1995) that states that Haldane's Rule will result if alleles affecting hybrid fitness are, for the most part, partially recessive. Based on this premise, differences in fitness seen between heterogametic and homogametic F_1 hybrid offspring are predicted to reflect differential expression of recessive gene effects, rather than a differential number of hybrid incompatibility genes having accumulated in the two sexes. Work focusing on autosomal patterns of reproductive isolation in *Drosophila* provides a means of testing which model best explains Haldane's Rule. Based on this research, no single explanation offered for Haldane's Rule so far is sufficient to account for all the data. These results support the hypothesis that Haldane's Rule actually represents a composite phenomenon.

Herbivory induced responses in plants; causes and consequences

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The regulation of plant modular structure has important but poorly acknowledge consequences for the evolution of plant resistance against herbivory. Regulation of plant functioning bases on two principles: on hormonal regulation by local meristems and on the hierarchy among meristems. Together these two factors may strongly modify the evolution of plant responses to herbivory. For instance, disturbances on plant apical dominance regularly increase the growth vigor of supressed meristems. Performance of herbivores on such tissues increases, as well as the probability of further herbivory. Since apical dominance is perhaps the most important organizing principle of plant growth, that may strongly constraint plant means to escape from such a potentially deleterious interaction. Furthermore, the assumed defensive responses of plants also may simply result from plant internal regulation. For instance, herbivore damage may hinder the development of plant primordial meristems and, as a consequence, the growth vigor of new sinks decreases. This has been shown to deleteriously affect herbivores.

A general ad hoc assumption in plant/herbivore studies is that herbivory and the responses of plants to herbivory have a causal relationship, and they can be explained on the basis of a cost/benefit function. Although it is clear that plants have 'truly' defensive responses against herbivores, overlooking the constraints caused by the internal organization of plants may easily lead to false assumptions of evolution of plant resistance against herbivory.

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Hormonal responses of black grouse Tetrao tetrix males to the presence of competitors and females

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Several studies have shown a relationship between the plasma concentration of androgen hormones and mating success of males. However, high testosterone level may be a consequence of mating success through the stimulation by females. In addition, successful males are often intensively challenged by other males, which may also induce testosterone secretion. I studied captive, lek-breeding black grouse (Tetrao tetrix) to test whether social stimuli influence testosterone levels of males. The males were exposed to different social situations (another male, a female, and an empty cage), and their plasma testosterone levels were assayed. When a female was presented in a nearby cage, the focal males had significantly higher testosterone levels compared to presentations with a male or an empty cage. However, there were no significant differences in the change of testosterone level. Additionally, I examined the possible physiological costs involved in testosterone secretion. The mean testosterone levels during the study correlated with the loss of body mass during the same period. The loss of body mass, in turn, was related to the onset of moult in autumn. These physiological effects indicate that there may be costs of testosterone, and ultimately, costs of hormone-regulated sexual traits.

Evidence for a selectively favourable reduction in the mutation rate of the rodent X chromosome.

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The evolution of the mutation rate is central to many fundamental evolutionary issues (e.g. the evolution of sex, of genome size, of individuality etc). The equilibrium per genome mutation rate has been hypothesised to result either from 1) a trade-off between the benefits of reducing the deleterious mutation rate and the costs of increasing fidelity or 2) a physiological constrain on the efficiency of repair/replication or 3) the effects of selection favouring lineages with higher rates of adaptation. For sexual organisms the latter argument is group selective and not supported by modifier analysis. From analysis of costly modifiers of the mutation rate, we show that the trade-off theory predicts a lower mutation rate of X-linked genes under certain conditions. This stems from the fact that deleterious recessive mutations on hemizygous chromosomes, are more exposed and hence, when they occur impose a high cost. We test this hypothesis by examination of 33 X-linked genes, that have been sequenced in both mouse and rat, and compare their rate of evolution against 238 autosomal genes. We find that the X-linked genes have a significantly lower rate of synonymous substitution. Neither the supposed higher mutation rate in males nor stronger purifying selection against slightly deleterious mutations on the X can adequately account for the low value. The most parsimonious explanation is that rodents have a lower mutation rate on the X chromosome than on autosomes. It follows that previous indirect estimates of the excess male mutation rate are inaccurate. Indeed, after correction we find no evidence for a male-biased mutation rate in rodents. This conclusion is supported by the finding that the rate of synonymous substitution in Y-linked genes is not significantly different from that in autosomal ones. We hence argue that, at least in sexual species, the mutation rate is determined by a trade-off between costs of reducing the mutation rate and the costs imposed by new mutations.

The use of archived fish otoliths to assess the genetic impacts of over-fishing.

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Biodiversity plays a central role in evolutionary biology, and its loss through anthropogenic activities has become a key issue in recent years. This decline has perhaps been most evident where complete ecosystems have been lost through such activities as agriculture, water management, urbanisation, and pollution. However, biodiversity faces a new threat in the form of intense large-scale exploitation of the biota . Over-harvesting is exerting unnatural selection pressures upon many species of fauna and flora, and driving some to extinction, while others experience dramatic population crashes. This is particularly true of marine fisheries which are still relatively understood, despite being the dominant major food source harvested from a natural population.

Much of the theory suggests that populations which are subjected to strong selection pressures or undergo substantial population declines, will experience a reduction in genetic diversity through the erosion of heterozygosity and polymorphism. Many of the recently developed models and laboratory-based experiments appear to support this theory, however, there is little conclusive evidence obtained from natural populations especially with reference to marine species.

As part of my PhD, I propose to investigate a series of fish species, resident in U.K waters, which have shown evidence of a phenotypic response to intensive over-fishing. I am currently developing protocols to extract DNA from otoliths which date back to a period prior to the onset of large-scale exploitation, and hope to highlight any changes in genetic diversity which may have occurred.

MULTIPLE MATING WITHOUT REGRET? EVIDENCE FROM FEMALE *DROSOPHILA MELANOGASTER*

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Multiple paternity and sperm competition in *Drosophila melanogaster* has been of continuous interest in evolutionary biology. Recently, it has been shown that seminal fluid transferred to the female significantly reduces female viability. Hence, females are expected to keep the number of matings to a minimum. However, if multiple matings represent a potential benefit for females, multiple mating may be beneficial under certain circumstances. Therefore, we used highly polymorphic microsatellite markers to determine the minimum number of mates of females collected in the wild.

Drosophila melanogaster females were caught from a natural population in Vienna. 90 female offspring of each female were analyzed for seven x chromosomal microsatellite loci. For all females we detected concurrent multiple paternity. Comparisons between offspring which hatched at different times did not show a significant pattern. Multiple paternity could be observed among the offspring. There was no significant correlation between multiple paternity and the order of hatching observed. However, a slight increase in the number of fertilizing males was observed towards the end of the study period. In total, we detected offspring of three to eight males in a single female.

Our data indicate that the number of matings can be much higher than required to provide sufficient amounts of sperm to fertilize all eggs. Hence, we conclude that either females gain a selective advantage by multiple matings or that the effect of multiple matings on female viability is much lower in natural populations than previously assumed. The latter explanation is supported by the observed coevolution between females and males.

The quantitative characters as a markers of population differentiation in mosquito larvae

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The variability of quantitative morphological characters in mosquito larvae of the Aedes genus can mark various types of population differentiation. The first group of characters with a fairly complicated morphological structure and significant functional loading is a matter of difference between populations from distant regions. Sometime this may occur in the same population in different habitats. Difference of these characters is usually formed only in the end of larval stage. The other group of characters including morphologically complicated ones reflects the stable intrapopulation variability that occurs in most populations of different species of this genus. This variability reflects a degree of preference for one of available alternative feeding strategies. Many of other behavioral and physiological peculiarities of mosquito larvae and imago are associated with this morphoecological trophic complex. In this group of morphological characters, the differences appear in the middle of larval stage. The frequency distributions of such characters belong not to normal but to bimodal type. Genetic variance of such characters is significantly greater than of others. At last, the variability of some simple quantitative characters with low heredity reflects the difference between species and appears at early larval stages. In general, the role of morphological characters as a markers of population differentiation is determined by their morhpogenetic modes, their position in morphoecological trophic system as a whole, and by the direct effects of natural selection.

How to exploit a patchily distributed resource

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When exploiting a resource patch in the absence of competitors, evolution often maximises the population numbers through maximising the efficiency with which resources are converted. When consumers with different characteristics share a patch it is not obvious what the outcome of the evolutionary process will be because the fitness of a certain strategy will depend on the strategies of its competitors. A strategy that maximises the use of the resource can easily lose to a strategy that wastes the resource when they share a patch. This problem is related to the evolution of altruistic traits or more specific to the exploitation of a host by parasites and the evolution of virulence. In these cases the question is whether a strategy can evolve which produces fewer offspring in a patch but from whose presence all other occupants in a patch benefit.

I have formulated a mathematical model for a population feeding on a patchily distributed resource. It is assumed that in such a population a rare mutant can appear with a different feeding rate and conversion efficiency. The fitness is defined as the rate with which a mutant can invade and is thus derived from the biology. The ESS's can be calculated after a trade off between feeding rate and conversion efficiency is assumed.

Whether or not a strategy can be invaded is mainly determined by the population sizes it can reach. A strategy that maintains low densities will leave a relatively large number of patches in which no eggs are laid at all. A mutant strategy that has less offspring in patches it shares with the resident can invade such a population if it finds enough patches in which it encounters no residents. Prudent strategies (strategies with a combination of low feeding rate and high conversion efficiency) therefore evolve under low food regimes, when food is abundant wasteful strategies prevail. Most importantly, this demonstrates that in a biologically realistic model altruistic, or non-virulent strategies can evolve relatively easily.

The role of female search behaviour in determining host plant range in plant feeding insects: a test of the information processing hypothesis

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Recent theoretical studies have suggested that host range in herbivorous insects may be more restricted by constraints on information processing on the ovipositing females than by trade-offs in larval feeding efficiency. We have investigated if females from polyphagous species have to pay for their ability to localize and evaluate plants from different species with a lower ability to discriminate between conspecific host plants with differences in quality. Females of the monophagous butterflies *Polygonia satyrus*, *Vanessa indica* and *Inachis io* and the polyphagous *P. c-album* and *Cynthia cardui* (all in Lepidoptera, Nymphalidae) were given a simultaneous choice of stinging nettles (*Urtica dioica*) of different quality. In addition, the same choice trial was given to females from two populations of *P. c-album* with different degree of specificity. As predicted from the information processing hypothesis, all specialists discriminated significantly against the bad quality nettle while the generalists laid an equal amount of eggs on both types of nettle. There were no corresponding differences between specialist and generalist larvae in their ability to utilize poor quality leaves. Our study therefore suggests that female host searching behaviour plays an important role in determining host plant range.

Working title: Evolution of growth forms in *Aeonium* (Crassulaceae).

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In the framework of plant architecture and modular plant growth 21 Canarian species of the genus *Aeonium* (Crassulaceae) are investigated to map and compare rules of growth. Parameters investigated are branching angle, shoot length and diameter and probabilities of branching, flowering and dying. Also roset morphology are quantified. It is hypothesized that simple rules predict the whole-plant morphology of the members of this genus ranging from few years old monopodial monocarpic species to sympodial polycarpic species of old age. The speculations up until now on the evolution of growth forms within the genus by adaptive radiation and separation of islands are taken further by comparing these growth models using the existing phylogeny of the genus.

Results will be presented at the Congress.

Keywords: *Aeonium*, Plant Architecture, Developmental Morphology, Canary Islands.

Evolution of dispersal: The impact of the temporal order of dispersal and reproduction within the life cycle

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Using a simulation model we examine how the temporal order of dispersal and reproduction within the life cycle may affect the evolution of dispersal strategies. We consider a spatially structured population and study the competition of genotypes that differ in their dispersal strategies but have the same local dynamics. We demonstrate that the evolutionary outcome depends significantly on the temporal order of dispersal and reproduction within the life cycle provided that: (1) density dependent dispersal strategies are involved into competition and (2) the environment is temporally variable. Our results suggest that selection can act in different directions depending on the timing of dispersal.

Love, songs and Drosophila: Evolution of dialects in D. teissieri

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Film video Pal in english which lasts 21 mn. Scientific Direction: Paillette Madeleine, Joly Dominique, CNRS - UPR 9034. Film director: Devez Alain, CNRS - ECOTROP URA 1183, 4 Avenue du Petit Châateau, 91 800 Brunoy. Production and distribution (sale and rent): Service Audiovisuel du CNRS, Meudon.

This film has to be replaced in the context of evolution and biodiversity. One might expect that acoustic variability of signals during courtship could have a key rule in population maintenance or divergence.
Here we present analysis of courtship sounds and related parameters on populations of D. teissieri. As a result of its strict forest-dwelling habitat this species has been most sensitive to reiterated forest fragmentations since Pleistocene times. In fact its present day distribution matches closely that of the extant African rainforest. Intra-specific differentiation has been investigated between two geographically isolated populations, one from Brazzaville (Congo), the other from Silinda (Zimbabwe). Courtship behaviour with synchronous songs, recording and analysis of the sound are shown. Sexual songs were analyzed in details (23 parameters) in addition to certain related to sexual activity (5) and wing morphology (5). In the three topics, parameters are differentiated between the two populations. As in other Drosophilidae, there are two types of courtship songs resulting from wing vibration: the Love Song, and the Sine Song. Love Songs from Brazzaville are longer than those from Silinda with a tendency to smaller and more regular inter-pulse intervals. The Sine Songs (SS) are about six times longer than the Love songs in each population, with an adaptation of their length to the receptivity of the female in Brazzaville. The Brazzaville flies show a greater acoustic activity and mates more readily than the Silinda ones. Their wings are slightly shorter and wider than those from Silinda. The roles of acoustic parameters in the recognition of the sexual partner in the context of incipient speciation are discussed.

Sperm heteromorphism: sexual conflict for the control of paternity

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Growing attention has been paid in recent years to the relative roles of sperm quality versus sperm quantity in sperm competition, which in turn has long been evidenced as one of the major components of sexual selection. Sperm size is one aspect of sperm quality which has acquired a special importance in fruitfly evolution. A striking diversity of alternative species-specific anisogamous strategies has evolved within the genus *Drosophila*, among which the 'all-short' or the 'all-giant' sperm strategies. The focus here is on still another evolutionary innovation consisting in the concomitant production of two sperm length classes by one male. Such innovation is shared by all the species of the *Drosophila obscura* group analyzed so far and has uniquely evolved in only one species, *D. teissieri*, in the *melanogaster* group (*melanogaster* subgroup). However, if species of the former group invariably exhibit perfect sperm heteromorphism (no overlap between short and long sperm length classes), the latter shows imperfect sperm heteromorphism (bimodal distribution). Another difference concerns the position of the nucleus that permits to discriminate between short and long sperm of the *D. obscura* group species while not in *D. teissieri*.

Alternative interpretations are discussed where sperm competition is assumed to be the driving force shaping the sperm length distributions. The cooccurrence within ejaculate of two generally clear-cut sperm morphs allows a subtle game based on sperm quality. But who plays? Males or females? The assumption is made that two selective forces operate independently: the target of selection acting in male-male competition would be sperm length, whereas the target of selection acting in sperm competition mediated through female choice would be sperm number. Data indicate that regardless of their length sperm are structurally and physiologically very similar, but on the other hand there is only clear evidence that long sperm do fertilize, especially in the *D. obscura* group species. We here hypothesize that long sperm would be fertilizing and involved in male-male competition while short sperm would primarily be devoted to confuse the female control of paternity. It is therefore suggested that the coexistence of two sperm morphs in one ejaculate would reflect a sexual conflict for the control of paternity.

Preferred patterns of food webs - a reliability theoretical analysis

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Food web graphs represent the pathways of matter and energy flows in ecosystems. Our aim was to analyse food webs from a reliability theoretical view. We have made our computations in a graph model. We have investigated the reliability of flows in various food webs, both in hypothetical ones and in real cases. Reliability depends on the probability of failures of edges and points in the food web graphs. We present some property of an optimal flow network and distinguish between different patterns containing a given number of points (populations) and levels. We suggest that various species differ in importance from a reliability theoretical view and determine key species. In our model the importance of key species depends not on their properties but on their position in the food web.

These results may be relevant for biodiversity conservation projects. The question of optimal food web patterns is analysed in the context of community evolution. We propose a hypothesis for the emergence of preferred food web patterns in evolution.

Phylogeography of darkling beetles endemic to the Canary archipelago: a comparison with the volcanic evolution of the islands

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We have investigated the phylogeography of saprophagous flightless darkling beetles, *Pimelia* and *Hegeter*, endemic to the Canary Islands using a fragment of the mitochondrial cytochrome oxidase I (COI) gene. The results are analyzed using approaches which allow inferences to be made about the population genetic structure and the mitochondrial genealogy of these beetles. In Tenerife, the species of *Pimelia* show two ancient mtDNA lineages which coincide with the disjunct volcanic evolution of the island. On the other hand, the intraspecific genealogies of *Hegeter politus* in Eastern islands of Fuerteventura and Lanzarote suggest a colonization in a north-north-east direction compatible with the geological ages and vulcanism of various parts of these islands.

Density-dependent survival of adult and sub-adult multimammate rats

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Population dynamics in strongly seasonal tropical environments is often assumed to be dominated by density-independent processes. The result of statistical modelling of Capture-Mark-Recapture data on the multimammate rat *Mastomys natalensis* from Tanzania show that (i) females survive better than males, sub-adults survive better than adults; (ii) temporal variation of survival of all individuals is similarly affected by the rainfall in the month; beyond this common pattern of temporal variation, we show that (iii) sub-adults exhibit a strongly density-dependent low persistence rate in the population immediately after their first capture; (iv) sub-adults survival in later months is, however, positively related to density; (v) adult survival shows negative density-dependence. By identifying ecological factors specific to functional classes, we are able to narrow down the possible mechanisms behind density-dependence.

Plasticity in the expression of genes that govern chemical defense in Trifolium repens (L).

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A longitudinal study of the amounts of cyanogenic glucosides and b-glucosidase in T.repens has shown that the greater part of the variation is due to differences in gene dosage of the genes Ac and Li. Ac is responsable for the production of the cyanogenic glucosides linamarin and lotaustralin; Li is the structural gene for linamarase. Another part is due to variations in modifiing genes. However, fluctuations in the environment play a role as well. This can be shown by the correlations between i.e. the concentration of cyanogenic glucosides on one hand and temperature temperature, relative humidity and photosynthetic active radiation in the 9 days preceding the collection date of individual leaves on the other hand. These correlations are dependent on the genotype: Clones with the same dosage of Ac, but a different genetic background may react differently to any one environmental factor. As there is an appreciable amount of variation between leaves of the same genotype collected on the same day, there is as yet an unexplained factor in the variation. This may in fact be a factor internal to the plant. The consequences of internally driven variation in the level of chemical defense will be discussed.

Life history modification of Silene latifolia (Caryophyllaceae) parasitised by the anther smut fungus Microbotryum violaceum

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Parasites induce changes in their hosts. This can be viewed either as pathological effects of infection, i.e. symptoms, adaptive defence by the host, or adaptive manipulation on the part of the parasite. Since parasites and hosts are involved in a coevolutionary arms race, it is not obvious which of the players has the upper hand at any given time.

The pollinator-borne anther-smut fungus Microbotryum violaceum is a prevalent parasite of the common roadside weed Silene latifolia (Caryophyllaceae). This fungal disease alters host plant phenotype in several important ways. Disease retards flowering in those male plants that initiate flowering in their first season, and increases the number of flowers produced by both male and female plants. Different fungal strains differentially augment flower production, suggesting that there is genetic variability for important fitness-related life history traits in natural populations of the fungus M. violaceum in Europe. Diseased plants also produce smaller, more irregularly shaped flowers with different nectar production than healthy plants, and the magnitude of some of these effects of disease differs for the different plant families or fungal combinations. Furthermore, in this short-lived perennial host plant, diseased plants were more likely than were healthy ones to initiate flowering in their first growing season. Since this shift from vegetative growth to reproduction should enhance fungal reproductive success, we interpret this as a manipulation of the host plant phenotype by the fungus to enhance fungal reproductive success.

Local adaptation in the anther smut fungus Microbotryum violaceum and its host plant Silene latifolia

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The outcome of the coevolutionary arms race between hosts and parasites depends on the ability of each player to respond to evolutionary changes in the other. This evolutionary potential depends on the rate of genetic change produced by mutation and sexual recombination. In addition, the rate at which resistance and virulence genes are exchanged among local populations may be important if host and parasite gene pools are subdivided. Parasites are generally assumed to evolve faster because of their shorter generation time, larger population size, and higher migration ability. This should result in parasite populations adapted to locally abundant host genotypes.

We investigated local adaptation in the anther smut fungus Microbotryum violaceum and its host plant Silene latifolia. The fungus sporulates in the anthers of diseased flowers and spores are transmitted to new infection sites by insect flower visitors. Since pollinators discriminate against diseased plants, transfer of host genes (i.e. pollen) between populations may occur more often than does that of fungal genes (spores). Furthermore, human activities, such as roadside mowing, may generate substantial seed dispersal. Therefore, in this system, hosts potentially migrate faster than parasites thereby preventing local adaptation of the parasite.

We collected seeds and fungal spores from 14 natural populations from a metapopulation. We inoculated seedlings from each plant population with fungal sporidial suspensions derived from the same population, from a near-by population (< 5km distance), and from two populations at an intermediate (< 30km) and remote (> 60km) distance. We compared subsequent infection success (proportion of diseased plants) of sympatric versus allopatric plant-pathogen combinations and analysed the relationship between infection success and geographic distance between plant and fungal populations.

C. ELEGANS AS A MODEL FOR GENETIC MAPPING OF LIFE-HISTORY TRAITS

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The nematode *Caenorhabditis elegans* offers perspectives for genetic mapping of life-history traits. Self-fertilizing hermaphrodites and males from different strains allow for rapid crossing and inbreeding (99% homozygosity) without inbreeding depression. Mapping is facilitated since *C. elegans* has a relatively small genome (100 Mb) which is expected to be sequenced completely in 1998. All information pertaining to the genome is publicly available in the ACeDB data base. Various strains differ widely based on assessment of markers and QTLs affecting fertility have already been mapped in *C. elegans* using transposon based sequence tagged sites (STS) in inbred strains. Since detection of putative QTLs is enhanced by using saturated linkage maps, amplified fragment length polymorphisms (AFLP) is a technique of great promise, yielding a virtually unlimited number of co-dominant markers. The aim is to map phenotypic plasticity to temperature in life-cycle traits of *C. elegans*, e.g. determination of QTL-environment interaction. This can be achieved through mapping inbred lines using STS and AFLP markers and association with trait values at different temperatures. The use of AFLP markers further facilitates the detection and isolation of genes associated with plasticity.

Response to selection for body weight in inbred mice: involvement of major genes

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Large-scale experiments by C. López-Fanjul and colleagues (*Genet. Res.* **62:** 107 (1993)) and T. F. C. Mackay and colleagues (*Genetics* **136:** 937-951 (1994)) in which initially inbred lines of *Drosophila* have been divergently selected for bristle number traits have produced spectacular selection responses largely explained by new mutations with extremely large effects. I have carried out a selection experiment in mice on body weight at 6 weeks with an inbred strain as the base population. The experiment has run for nearly 50 generations (10 years), and large responses to selection have occurred. The pattern of response is strikingly similar to the *Drosophila* bristle experiments, with strong asymmetry and the appearance of bursts of selection response followed by plateaus, presumably due to the rapid fixation of mutations with large effects on the trait. Unexpectedly, the major part of the selection response has been upwards, and appears to be due to a single mutation. In contrast to the *Drosophila* bristle selection experiments, in which recessive lethal mutations with large bristle effects made major contributions to the response and led to reductions in fitness, directional trends in fitness traits were not observed. However, artificial selection for body size was very weak in the mouse lines, as family sizes were small. The lack of change in fertility in these lines is at odds with recent concern that small populations may be vulnerable to extinction due to "mutation meltdown" (R. Lande *Conserv. Biol.* **9:** 782 (1995); M. Lynch *et al. Am. Nat.* **146:** 489 (1995)). The selected mouse lines actually showed a slight increase in fertility, and the data are consistent with a *maximum* directional mutational input for fertility per generation (product of genome-wide mutation rate and mean mutation effect) of about 0.1% if a model with equal mutation effects is assumed, or about 0.4% if a gamma distribution of mutation effects is assumed.

The origin of insect societies

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Until recently two research traditions have proceeded independently in seeking explanations for the evolution of eusociality. Traditionally, the study of genetic factors has been prominent in insect research, whereas vertebrates studies have focused on the role of environmental factors. Yet, it is now clear that ecological and genetic factors both influence the evolution of reproductive altruism. Skew models allow to consider simultaneously genetic and ecological factors by analysing 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 cooperation between animals. Skew models can be used both for invertebrates and vertebrates and examples will be given to illustrate the power of these models.

A genetic model for reinforcement of mating preferences on an island

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We present an analytic model for the evolution of premating isolation in an island population. The model allows for any type of female mating preference, and any number of genes influencing the preference, the male mating display traits, and the characters that cause postmating incompatibility. We allow incompatibility to result from either sets of epistatically interacting genes (as found in *Drosophila*) or from ecological factors that decrease hybrid fitness (as found in several vertebrate species).

The model asks how a mating preferences on an island evolves to discriminate against males that migrate from a continental population. The degree of reinforcement can be predicted largely in terms of phenotypically-measurable quantities, such as the number of phenotypic standard deviations between the mean display trait on the island and continent.

Three major results are, first, that reinforcement will occur if the mean display trait differs on the island and continent, even if there is no postmating incompatibility. This outcome results from a kind of good-genes effect, in which island-specific preference genes hitchhike in association with island-specific display trait genes. Second, reinforcement is enhanced by both epistatic or and ecological post-mating incompatibility. Epistatic incompatibility, however, has a larger impact than ecological incompatibility. Third, incompatibility effects that act late in the life cycle (such as infertility) promotes reinforcement more strongly than those that act early (such as embryonic defects).

Optimal investment in maintenance as a function of physiological state

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The allocation of metabolic resources to processes of somatic maintenance is of key importance in determining how long an organism can survive before it succumbs to an accumulation of random damage. The disposable soma theory of senescence suggests that because of the competing demands of growth and reproduction, less effort is invested in maintenance of the somatic tissues than is necessary for indefinite survival. Strategies for optimal investment in somatic maintenance may be influenced by the organism's current physiological state and by environmental factors such as the availability of nutrients. We describe approaches to state-dependent optimisation of investment in maintenance that have been used to examine whether the phenomenon of life span extension due to calorie restriction in rodents may have an evolutionary basis. For example, it has been suggested that a transient period of famine in the natural environment may favour a temporary upregulation of maintenance functions and shut-down of reproduction to enable the animal to survive in good physiological condition in order to maximise reproductive potential when the period of famine is over. Our model demonstrates that in some circumstances this strategy will be favoured by natural selection. It identifies key physiological parameters that determine whether or not this is the case. The model can thus aid in considering whether life extension through calorie restriction is expected to occur in other mammalian species. State-dependent optimisation of investments in maintenance versus reproduction may also be important in determining optimal schedules of reproduction, including the terminal shut-down of reproductive function as occurs in the human menopause.

The optimal timing of reproduction of semelparous perennials in temporally heterogeneous environments.

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To study the optimal timing of reproduction we try to answer the following questions: 1. What are the underlying physiological mechanisms controlling the timing of reproduction in semelparous perennials? i.e. what are the characters under selection? 2. Are there between and within populations genetic differences in the timing of reproduction? 3. What is optimal timing of reproduction and how does it depend on environmental conditions? 4. Can we predict and explain genetic differences in timing of reproduction between habitats? We studied several semelparous species in 100 local populations in a coastal dune area in the Netherlands. All these species can only flower and reproduce after winter cold. In addition they have a minimum size for flowering. Our demograhic study shows that age is not correlated with the probability of flowering. The timing of reproduction should therefore be studied as a size rather than an age-structured problem. For Cynoglossum officinale we found large differences in the minimum size for flowering both within and between populations. Selection experiments showed that it is easy to select for a smaller or larger minimum size, even after one generation of selection large differences are found between selection lines. An optimization model for our study area showed 1. there exists a unique optimal value of minimum size for reproduction. 2. there is weak selection against flowering at sizes larger than the optimal size but strong selection against flowering at smaller sizes. 3. the predicted optimal value is close to the value at which 50% of the plants reproduce in the study area. 4. The optimal size for reproduction is mostly determined by the size-dependent increase in the expected number of seeds and less by the effects of averaging variable recruitment over years. Comparison of a dune area in England with our study area showed that in England, individuals of Cynoglossum officinale flowered at a larger size. This can be explained by a lower mortality and a higher growth of non-flowering plants.

Evolution of sex: Anti-genomic-parasite hypothesis

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An important issue in modern biology is our failure to adequately explain the forces underlying the evolution and maintenance of sex. Sex, defined here as crossing-over associated with outbreeding, is an ubiquitous process found in the meiosis of most eukaryotes as well as in bacteriophage infection. One possibility is that sex represents a defense mechanism against ever-changing parasites. It is not clear whether the products of most of the genes are involved in a specific relationship with parasites' gene products. Here I present a hypothesis that sex is a strategy to fight with genomic parasites that directly attacks genes as opposed to their products.

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Evolutionary aspects of the malaria life cycle

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Malaria parasites have a complex life cycle involving several distinct stages in two hosts. Only recently have there been any attempts to understand the life cycle from an evolutionary viewpoint. I will discuss two aspects, where we are beginning to understand some of the evolutionary pressures forming the complexity of the life cycle: the growth of the parasite within its vertebrate host and the effect of the parasite on its mosquito vector.

The within-host dynamics are characterized by the replication of the parasite in red blood cells and by the production of distinct stages that are involved in the transmission from the vertebrate host to the mosquito. By assuming that transmission to mosquitoes is maximized, one can predict the timing of production of transmission stages as a function of the parasite's replication rate and virulence. These predictions largely hold among and within malaria species. They can also help to understand the transmission differences among drug resistant and sensitive strains of malaria parasites.

In the mosquito vector, malaria infection shortens the life-span. The parasite's virulence is at first sight mal-adaptive, as its transmission success depends on the mosquito's surviving to bite the next host. It can, however, be understood from the association between biting and mortality. Blood-feeding is not only necessary for the mosquito to reproduce, but also imposes a major risk because of the bitten individual's defensive behavior. Therefore, if the parasite can manipulate the mosquito's blood-feeding behavior to enhance its transmission, we would expect it to reduce the mosquito's biting rate during the early stages of the parasite's development (when it cannot yet be transmitted) but to increase it when transmission is possible. This is the pattern observed in field and laboratory situations.

Is longevity a sexually selected trait?

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According to the handicap principle of sexual advertisement, females prefer male traits that function as viability indicators. The indicator will honestly reflect male quality, if costs prevent low-quality males from developing it. The observation that oldest males often give the most intense signals gives rise to two questions. (1) Can old age as such function as a viability indicator, signalling the ability to survive up to that age at least? (2) If male advertisement effort is age-dependent but male genotypes hardly change during lifetime, strict correspondence between phenotype (advertisement) and genotype (genes for viability) breaks down. Is honesty maintained in such a case, i.e., can the females still use the advertisement to choose males with 'good genes'?

I show that viability differences caused by recurrent mutations in polygenic traits can lead to oldest males having highest fitness mean. The conclusion is very similar in constant, variable, and continuously evolving environments. Old-age preferences in females therefore indirectly suggest that mutation-selection balance is strong enough to generate heritable variations in fitness without additional mechanisms such as environmental variation or host-parasite coevolution. However, forms of trade-off functions between reproductive effort and survival ultimately determine whether the genetic quality of a male is reflected in longevity as well. The second question requires considering viability costs of male advertisement explicitly. I show that strict honesty is not always maintained in life history optimization: the highest advertisement intensity or, alternatively, the longest lifespan may be associated with a low-quality male. However, honesty in maintained in an average sense over the lifetime of an individual: survival up to age classes with dishonest males will be very small. High quality males will always be able to choose a life history that makes them more prevalent as mates, so that it remains optimal for females to rely on the advertisement signal even if it is not completely honest.

Parent-offspring conflict over sex-ratio bias in co-operatively breeding vertebrates

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According to Fisher's equilibrium sex-ratio theory, when daughters and sons are of equal reproductive value, parents should adjust the production of their offspring in such a way that the average fitness costs of sons and daughters are equal. This means that if ecological or social factors increase the fitness costs to the parents of one sex relative to the other, parents should discount these costs by producing fewer individuals of the more costly sex. Offspring can decrease their individual costs to parents through local-resource enhancement (e.g. helping their parents to raise later offspring). Conversely, they can increase their costs by competing with the parents for access to essential resources. Using recently available molecular tools to determine primary sex ratios in bird species it is shown that in some bird species local resource enhancement and competition, are selection pressures that affect primary sex ratios. In several bird species females bias the sex of offspring in order to increase their lifetime fitness. The manipulation of the primary sex ratio is adaptive from the perspective of the breeding female. However, it is not known if this sex manipulation is also adaptive for the breeding male or for the offspring. In this paper I will discuss the question of whether there is parent-offspring conflict over sex-ratio bias in bird species.

Effects of food plant on wing pattern induction in the tropical butterfly *Bicyclus anynana* (Butler)

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Bicyclus anynana shows phenoptypic plasticity in the form of seasonal polyphenism. The butterflies show strikingly different wet- and dry season forms. These forms are primarily under the environmental control of temperature and larval development time. Food plant quality effects the larval development time. It appears that interspecific differences in food plant quality influence the development of the wing pattern, indicating that this could be an important biotic factor influencing the reaction norm in the field.

Development of parasitic potency and reproduction of nematodes exposed to certain sub-lethal nematicide concentrations.

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Parasitic potency (eggressiveness), fecundity and reproduction of root-knot nematode, Meloidogyne incognita generating from parents exposed to sub-lethal concentrations of each of oxamyl (Vaydate24%L) and ethoprophos (Mocap 10% G) were studied on tomato .

Individuals generating from exposed parents were more aggressive than that generating from non-exposed individuals either in the first generation (F_1) or in the second generation (F_2). Reproduction potency of nematodes exposed to 50 ppm oxamyl and 50 ppm ethoprophos increased by 35.8% and 51.7% over control in F_1, respectively. While, it increased by 35.6% and 47.4% over control in F_2, respectively.

Fitness decrease due to accumulation of point mutations in mismatch repair deficient strains of yeast *Saccharomyces cerevisiae*

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Spontaneous mutations result from incorrect replication of DNA. Among several types of possible errors there are mismatches of single bases and deletions/insertions of one or few bases during replication. Mismatch repair restores the proper sequence of a daughter strand. Strains deficient in this type of repair are likely to accumulate spontaneous point mutations at a rate enhanced by about two orders of magnitude. Both the origin of mismatches and mechanisms of repair are similar in various DNA-based organisms. Therefore mismatch repair deficient strains of yeast provide well defined and typical material for the study of evolutionary consequences of genetic load.

In this experiment haploid strains of mismatch repair deficient yeast were propagated for several hundred of generations in a way promoting accumulation of mutations. Fitness of these strains, measured as maximum growth rate, declined gradually and was reduced by more than half by the end of experiment. The loaded haploids were then mated and fitness of the resulting heterozygous diploids was evaluated. The obtained data can be used to estimate the interaction of deleterious mutations between loci (epistasis) and masking effect within diploid loci (dominance).

Conflict in house mice: comparative analysis of social behavior in two sympatric related species: house mouse (mus musculus musculus) and mound-building mouse (mus spicilegus).

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Comparative analysis of social behavior in M. m. musculus (commensal species) and M. spicilegus (wild-living species) was conducted in semi-natural conditions. In the first experiment 14 groups each consisted of two males and two females were used. Groups were observed in enclosures (100 x 100 x 30 cm). In the second experiment six groups of different sexual composition (in whole 27 mice) were used. Groups were observed in large enclosures (20 sq.m). In latter case four groups consisted of unfamiliar individuals and two groups included familiar individuals of M. spicilegus were under study. Each familiar group consisted of individuals which lived before experiment in same natural mound and included all mice inhabited one mound. Comparison of social behavior in M. m. musculus and M. spicilegus demonstrated the similarity of relationships in groups consisted of unfamiliar individuals, hierarchical order were observed. Females of M. spicilegus were more aggressive as compared to females of M. m. musculus and they formed their hierarchical order. In groups consisted of unfamiliar individuals subordinate males and subordinate females were lost during three-twenty days after beginning of group formation. There were no agonistic interactions in groups consisted of related individuals captured in the same mound, but all mice were aggressive to intruders as males as females. All members of family groups exibited similar behavioral stereotypes. The differences were found in number and dynamics of their naso-nasal and naso-anal interactions. It is possible to suppose that there are no hyerarchy in groups of M. spicilegus in nature. Relationships of these mice in family groups are amicable. In special laboratory experiments seasonal differences of aggressive behavior in M. spicilegus was found. In mixed groups the dominant male can be M. m. musculus or M. spicilegus. Social status was determined by individual characters. There were no data indicating the dominance of one species over another. The social structure and role of aggressive behavior in societies of commensal and wild-living species of the genus Mus is compared in relation to their ecology and adaptations to living conditions.

Costs of sexual traits

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According to conditional handicap models, females use male sexual traits as honest signals of male viability. Models assume that sexual traits are costly and that they reflect male phenotypic condition. Despite the theoretical plausibility, empirical support for the models is scarce. We experimentally tested whether sexual signalling, drumming, in the spider *Hygrolycosa rubrofasciata* is a condition dependent, costly trait, and thus offers a honest signal of quality to females. Females prefer males with high drumming rate, and male drumming is positively correlated with male viability. Male body mass is not a target of female choice and body mass does not influence male survival. Male drumming was dependent on his nutritional status, and males that were experimentally induced to increase their drumming activity suffered increased mortality. We aimed to study the mechanisms underlying this increased mortality by measuring metabolic rate of signalling and resting males. Male drumming increased male metabolic rate 22 fold compared to resting metabolic rate. In addition, larger males had significantly higher drumming metabolic rate per mass unit than smaller males. Thus our results suggest that drumming of a male is a honest condition dependent signal of male quality causing increased mortality through increased energy expenditure. Interestingly, there is no correlation between male body mass and drumming activity, even if larger males suffer relatively higher energy expenditure than smaller males.

Correlation between virulence and vertical transmission and it's consequences on the evolution of a plant pathogen's virulence.

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Theoretical models predict that pathogens capable of vertical and horizontal transmission should evolve towards less virulence if they can achieve high vertical transmission with low virulence. The fungus *Atkinsonella hypoxylon* castrates the grass *Danthonia compressa* by preventing the development of the host's aerial inflorescences. Sporadically, partially castrated inflorescences are observed on infected hosts in the field. Hosts that are partially castrated suffer a lower reduction in fitness than completely castrated hosts. If partial castration is determined by the fungal genotype, and selection favors lower virulence, why are partially castrated plants rarely observed? We investigate the occurrence of partial castration in *D. compressa* plants inoculated with 3 fungal strains, and found that partial castration occurred primarily in plants inoculated with one strain. We also investigated vertical transmission to seeds and seedlings in partially and completely castrated plants. The fungal strain that causes partial castration was also less efficient at being vertically transmitted. This correlation between low virulence and low vertical transmission might explain why less virulent strains are not commonly observed. We also found that the proportion of vertically infected seeds was higher than the proportion of infected seedlings derived from these seeds, indicating that the presence of fungi in the seeds does not characterize a complete vertical transmission event. Our results support some of the predictions of models on the evolution of parasite virulence, but also suggests that vertical transmission of plant pathogens are more complex than previously modeled.

Energy allocation between growth and reproduction: The Pontryagin Maximum Principle solution for the case of age- and season-dependent mortality

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Optimal allocation of energy to growth and reproduction was studied with a dynamic optimization method for long-lived animals inhabiting a seasonal environment. It was found that after maturation it is optimal to grow either several years (if the animals age in the sense that their mortality increases with age) or asymptotically (if there is no aging). Asymptotic growth can be well approximated with Bertalanffy's equation, even if the animals are able to grow to infinity. This is because it is optimal to allocate an increasing proportion of surplus energy to reproduction year after year following maturation. Age at first reproduction depends on mortality in both favorable and unfavorable seasons, and also depends on the favorable season length — it is optimal to mature early when mortality is high or the season is short. Size at maturity depends additionally on the parameters of the equation describing the size-dependence of the production rate. When mortality in the unfavorable season is high compared to mortality in the favorable season, a large part of growth is realized after maturation. The model qualitatively explains growth patterns and life histories in fish, reptiles, amphibians, and some long-lived invertebrates which grow after maturation. To understand better the diversity of life histories, field biologists working on such animals should focus on differences in the aging rate, favorable season length, mortality rates in both seasons and the size-dependence of production rate. Optimization models based on the allocation principle are promising tools to integrate these kinds of data.

Costs of resistance against parasites: trade-off between encapsulation ability and competitive ability

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Trade-offs have often thought to be responsible for genetic variation in resistance against pathogens and parasites within populations of animals and plants . Whereas in some plant species, trade-offs between resistance against pathogens and other fitness parameters have been shown to exist, evidence for fitness parameters trading-off with resistance against parasites in animals is very rare.

Drosophila melanogaster-larvae and one of their hymenopteran parasitoids, the braconid *Asobara tabida*, are used as a model system. *Drosophila*-larvae defend themselves against parasitism by a cellular immune reaction which leads to encapsulation and death of the parasitoid egg. Across Europe, a large amount of genetic variation is observed, both within and between populations, in their ability to encapsulate parasitoid eggs.

A large, field-collected population of *D. melanogaster* with a low average encapsulation ability was subjected to selection for increased encapsulation ability. Encapsulation ability in the selection lines increased from 5 to 60% in 5 generations; the control lines did not show a change. Subsequently, control and selection lines were compared in a range of life-history parameters. Under optimal circumstances, no difference between control and selection lines was found in any measured parameter. However, when larvae were reared under increasing levels of competition for food, larvae from the selection lines suffered a higher mortality than larvae from the control lines.

Thus, in *D. melanogaster*, the cost of resistance against parasitoids appears to be a reduced larval competitive ability. The magnitude of this cost, and thus the selection pressure against a high encapsulation ability in the absence of parasitoids, depends on the environment.

Differential growth and the evolution of sex chromosomes: a simulation study

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Sex determination in vertebrates is probably mediated by differential growth of the embryo. Evidence suggests that the activation of the cascade of events leading to testis or ovary differentiation depends on whether the undifferentiated gonad has reached a threshold size at a critical moment in development. Kraak & de Looze (1993: *Neth. J. Zool.* 43, 260-273) argued that genetic sex determination (GSD) evolves from environmental sex determination (ESD) if growth promoting genes take over the role of the environment in bringing about differential growth. They predicted that (1) the sex with the faster growth under ESD will become the heterogametic sex, and (2) the growth enhancing genes will become tightly linked on one chromosome that does not recombine with its homologue, thus resulting in sex chromosomes.

In this study we systematically investigate these verbal arguments by means of a population genetical simulation model. We consider a diploid population in which the sex of an individual is determined by its size (or growth rate) relative to a threshold value. Individual size is distributed around a genotype-specific average and hence partially under genetic control. Size has also sex-specific effects on fitness, such that the probability of survival to reproduction increases with size only or more steeply in the sex that arises at fast growth. We study single-locus as well as multi-locus control of growth, and we also consider a locus that determines the threshold value and a locus that controls the recombination rate between growth loci.

With one locus for growth, the locus may remain polymorphic under at least some conditions, and the fast growing as well as the slow growing sex may become heterogametic. In case the fast growth allele is (partially) dominant over the slow allele, the fast growing sex becomes heterogametic. With multiple loci for growth, only if one sex benefits from being small while the other benefits from being large, reduced recombination between the growth loci and heterogamety of the fast growing sex results. Under many starting conditions, however, no reduced recombination nor heterogamety occurs. The simulations show that the scenario predicted by Kraak & de Looze is feasible in principle, but less general than originally conceived.

Positive correlation between recombination rates and levels of genetic variation in natural populations of sea beet (*Beta vulgaris* subsp. *maritima*)

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Several theoretical models have been developed that focus on the relationship between the level of genetic variation and the amount of recombination per physical unit in a given genomic region. Both the genetic hitch-hiking and the background selection models predict a decrease in genetic variation in regions with low recombination rates. We have analysed two Italian populations of sea beet (*Beta vulgaris* subsp. *maritima*) and found a positive correlation between levels of genetic variation and recombination rates. DNA from eleven plants in each population was digested with two separate restriction enzymes and 27 markers from one linkage group of a sugar beet RFLP map were used to estimate levels of genetic variation in different regions. The varying degree of clustering of markers over the RFLP linkage map was used to estimate recombination rates in different regions. The correlation between the estimates of genetic variation and recombination rates was significant but only explained a small proportion of all variance in genetic variation among loci.

Triploidy in fire ants (*Solenopsis invicta*) associated with the polygyne social form.

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Ploidy level of fire ant females was studied using microsatellites. More than 10% of the workers and queens were triploid in polygyne (multiple-queen colonies) populations. By contrast, not a single triploid individual was detected in monogyne (single-queen colonies) populations. This difference in ploidy level between the two social forms might stem from the presence of diploid males in the polygyne form. Males are generally haploid in Hymenoptera but a recent bottleneck resulted in a dramatic increase in the proportion of diploid males in the polygyne form only, with 83% of the males being diploid. These males were thought never to produce sperm. However dissection of diploid males showed that 2.4% of these males indeed produce sperm. These diploid fertile males may thus be at the origin of the high level of triploid females in the polygyne form.

Single- and multilocus microsatellite variation in the Alpine marmot (*Marmota m. marmota*)

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As revealed by allozyme studies, the genetic variation is strongly reduced in Alpine marmots from Austria and Germany. Microsatellite analyses were carried out to investigate whether the genetic depauperation is due to a species wide bottleneck at the end of the last glaciation or to the impact of human acivities, e.g., founder effects in reintroduced populations.

The microsatellite loci detected by the DNA-probe $(ATCC)_4$ were used to investigate the variation in 4 authochthonous and 4 reintroduced populations. The authochthonous populations are thought to be direct descendants of the postglacial colonizers, while the allochthonous populations have been founded by small numbers of individuals released in the course of reintroduction efforts over the last 150 years. In the multilocus fingerprints, all 8 populations were found to be polymorphic but at a much lower level than comparable mammalian species. In spite of postulated founder effects the variation in the allochthonous population was not reduced compared to the authochthonous populations. Among the autochthonous marmots the population from the Central Alps of Switzerland showed the highest variation. This may be due to a higher number of individuals inhabiting a more homogenous range, which allows migration between populations. Thus these marmot populations may be less sensitive to reductions of their populations size by overhunting or high winter mortality. In the allochthonous populations the microsatellite patterns reflect relationships to the putative source populations of founder individuals.

In addition to multilocus fingerprinting, six new single locus microsatellites (CA/GT) were isolated and sequenced. PCR primers were designed to amplify these loci in population studies. The 8 populations already analysed with the multilocus method were reanalysed and a larger population sample from Switzerland was screened to confirm the higher variation found in the Central Alps.

The evolutionary implications of brain size reduction during domestication

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The central nervous system of placental mammals is, in general, built up according to a rather uniform grundbauplan. However, evaluated in more detail the diverse extinct and extant species have brains species-specifically evidently different in absolute and relative size, in form and outer appearence, in composition and proportioning of brain parts, in fissuration pattern and gyrification intensity of the forebrain hemispheres, in histological differentiation of certain structures and other parameters. These differences between species are to be interpreted as results of evolution and adaptive radiation linked by mechanisms of genetical diversification and special selective factors during phylogenetic events in connection with the origin of species. Evolution is characterized by body-size independent enlargement of total brain (cerebralisation, encephalisation) especially of the forebrain (telencephalisation) and the neocortex (neocorticalisation). Adaptive radiation into special ecological niches has on different evolutionary levels led to a rather similar and convergent enlargement of special functional brain structures (sensory, motoric, limbic, etc.).

Domestication has not led to an origin of new species although domesticated forms (e.g. pig, dog, etc.) are very different from their ancestral progenitors (e.g. wild boar, wolf, etc.) in nearly all biological parameters. Intraspecific comparisons of domesticated forms with individuals of common ancestry still living in the wild resulted in body-size independent smaller brain sizes in the former and in a different proportioning of brain parts. Thus, contrarily to evolutionary processes domestication is characterized by brain size decrease on a species level. However, less cerebralized species of the orders Rodentia and Lagomorpha show minor decrease values due to domestication to species-specific amounts of 0 % - 14 %, higher cerebralized species of the orders Artiodactyla and Carnivora of 18 % - 34 %. In most cases the neocortex is especially reduced in size. Besides these evolutionary implications several functional systems are convergently changed from wild to domesticated forms. Zoologically these effects can be evaluated as largely convergent adaptations of several species into a human-made ecological niche called domestication.

Genetic basis of inbreeding depression in *Arabis petraea*

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Segregation of marker genes and associations of marker genotypes with fecundity traits in selfed progeny of habitually outcrossing species can provide information on the genetic basis of inbreeding depression. We studied the genetic basis of inbreeding depression in the self-incompatible plant species *Arabis petraea*. Twelve selfed families were produced by breaking the self-incompatibility with bud-pollination. The parental plants were scored for 14 enzyme loci and 3 microsatellite markers. Early viability selection was examined by scoring marker genotypes of young seedlings. We found six significant deviations from 1:2:1 ratios at marker loci out of 60 tests in seedlings (10%). The observed genotype ratios were studied with a graphical analysis and a Bayesian method to distinguish between different modes of gene action at a linked viability locus. Four of the deviant segregation ratios suggested overdominance and one recessivity. Other components of fitness were examined through measurements of seed size, germination time, early growth rate, flowering time, and root and above ground biomass. We found only few significant linkages between marker loci and these fitness traits (19 out of 287 tests, or 6.6%). The failure in finding loci contributing to inbreeding depression in fitness traits, in spite of a presumably high inbreeding depression, indicates that these loci may have smaller effects than loci responsible for differences in early viability. QTL mapping of inbreeding depression with a dense marker map would give more power to detect the genes and examine their mode of action.

Adaptive acid tolerance response of Brucella.

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Bacterial adaptation in stressful environments is an important biological problem with applications toward understanding pathogenic microorganisms. Acid pH is an environmental stress often encountered by Brucella during both the "environmental" and the "pathogenic" stages of its life.

The behavior of B.suis 1330 and B.canis RM6/66 in acid conditions was investigated. In in vitro cell infection assays was found that B. suis 1330 is virulent while B. canis attenuated. This difference in virulence is interesting since on a genomic level B. suis 1330 and B. canis RM6/66 appear to be very closely related. B.suis 1330 was more resistant to low pH than B.canis RM6/66, which lysed at pH 4.6. Survival measured after 4 hours acid shock at pH 3.2 showed that the relative survival of B.suis 1330 was 1000-fold greater than that of B.canis RM6/66.
An adaptive acid tolerance response (ATR) was induced in both species by overnight culture at pH 5.8, however while the acid sensitive B. canis RM6/66 had more than a 2000-fold increase in survival following acid shock, the increase in survival of B.suis 1330 was only around 10-fold. The ATR system in B. suis is constitutively expressed at a low level which would also explain its increased acid resistance. In both species, the induction of the ATR was rapid, being evident after 30 minutes exposure to pH 5.8 and was maximal after 4 hours. The kinetics of the induction of ATR were followed showing that 4 hours at 5.8 were required for full protection.

At present using genetic approaches to investigate the mechanisms of acid resistance in Brucella is under way.

Dynamic cluster analysis of binary RAPD data suggests differentiation among endemic clupeid populations in Lake Tanganyika

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Dynamic cluster analysis developed for signal compression in image manipulation was applied to binary presence/absence matrix of 60 RAPD bands from 260 ***Stolothrissa tanganicae*** clupeids from Lake Tanganyika. High variation among pairwise similarity indexes among studied fish did not follow simple geographical or seasonal patterns. We tested, if the variation reflects existence of subpopulations.

Dynamic cluster analysis on supposed 1-12 subpopulations performed 20 iterations with 10 trial solutions generated in each iteration. In initial solution random individuals are representatives for each cluster. Other samples are assigned to clusters whose representatives are the closest. The trial solutions are generated by making random modifications to the current one: any population is made obsolete, and a new population created with a randomly chosen individual as representative. The samples are reassigned to populations by minimising the pairwise distance to the representative. The best solution minimising the intracluster diversity among the initial and the varieties is chosen to the next iteration.

To evaluate the number of subpopulations we compared the distortion value of the clustering with the random solution. Clustering data to four groups resulted the best ratio.

The resulting subpopulations had significantly different frequencies in 7 - 21 RAPD bands when compared to the pooled samples of *Stolothrissa tanganicae*. Members of clusters can be identified by their band frequencies, even though no clearly diagnostic fragments were found. This result was based on small sample size and can be used as a working hypothesis for further studies.

High polymorphism of the mitochondrial control region in Fennoscandian willow tits (*Parus montanus*)

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We studied the differentiation and dynamics of two Fennoscandian willow tit populations locating ca. 1000 km apart in Finland and Sweden by using the control region sequences of the mitochondrial DNA. Individual variation in the control region was extensive since all the 13 Finnish and the 12 Swedish individuals were different and the intraspecific variation measured as the pairwise genetic distance resulted in 0.08-1.09 %, averaging 0.52 %. In the minimum spanning network connecting the genotypes, the two populations were completely intermingled, showing no local geographic structure. This result was verified by the analysis of molecular variance which revealed no divergence among the populations.

The distribution of pairwise genetic distances for the combined data set was very close to the Poisson distribution, which is expected for an expanding population. This result was supported by significantly negative Tajima's D value. The migration rate indicates that 1) the effective population size of the breeding willow tits is surprisingly large and 2) the gene exchange between distant localities is extensive. Thus, the whole Fennoscandian population can be regarded as one panmictic unit, without any subdivisions to local demes.

The amount of gene flow is remarkable because the willow tit has been considered highly sedentary species performing only short distance dispersal. Provided that adult birds are site-tenacious, the efficient gene flow needs an assumption of widespread summer dispersal of juveniles and/or genetic effectiveness of the strong irruptive autumn invasions, monitored in the northern parts of the species range.

The Computationally Complete Ant Colony: A Framework for the Study of the Functional Organization of an Ant Colony

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We present a model to explain the global behavior of an ant colony from the behavior of the single ants. The model is motivated by observed behaviors of ants. Each ant has a finite number of internal states. An ant's internal state changes either by interaction with the environment or by interaction with another ant. In the model the colony's environment is observed by single ants, and the colony responds by changing the allocation of ants. We then study the sophistication of information processing such a colony is capable of and find it to be computationally complete. Comparing this model to a model without interaction among the ants shows that information sharing enables the colony to respond to its environment better. We present empirical results to substantiate the model, and make further empirical predictions. The model is then placed in an evolutionary framework with haploid/diploid dynamics, and we examine the ability of such colonies to adapt to their environment.

If the shoe fits, wear it: the influence of host life history on parasite life history

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We can categorize animals, according to their method of feeding, as predators, grazers/micropredators, typical parasites, parasitic castrators or parasitoids. These trophic strategies are typically categorical when applied to distinct ontogenic periods. What is responsible for determining the type of life history strategy an animal employs? Certainly, phlyogenetic constraints are important within clades. For example, many wasps are parasitoids because their ancestors were parasitoids. Also, some groups have structures that pre-adapt them to a trophic strategy, such as the ovipositor of ancestral free living wasps which probably aided the evolution of a protelean parasitoid lifestyle.

If we were able to hold phylogeny and morphology constant, we could examine how variation in host/prey life history traits should select for different feeding strategies in consumers. To evaluate this, I have constructed a series of simple models that evaluate the best feeding strategy for a given host/prey life history. The currency that I use for consumer fitness, is the amount of energy obtained in an average lifetime. For micropredators and predators, lifetime energy is the number of hosts successfully attacked multiplied by the amount of energy consumed per host. For parasites, lifetime energy is a function of the probability of finding a host, times the amount of energy that can be removed from the host. The main life history attributes that I evaluate are the host's life span, size, and reproductive tissue mass. Host size, for example, can affect the ability of the consumer to find a host/prey, its attack success and the amount of energy that can be consumed.

These models generate several predictions. Not surprisingly, the trade-off between, predation and grazing/micropredation is strongly influenced by prey size. Parasitism is a better strategy than micropredation in hosts that are long lived and large enough to resist parasite induced pathology. Parasitoids and parasitic castrators are favored when hosts are only slightly larger than themselves. Parasitic castration is more profitable in hosts that live long and invest a lot of energy into reproduction. These predictions seem relatively consistent with what we observe in nature.

The Evolutionary Consequences of Niche Construction.

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Organisms, through their metabolisms, their activities, and their choices, define, partly create, and partly destroy their own niches. This "niche construction" regularly modifies both biotic and abiotic sources of natural selection in environments, and generates new sources of feedback in evolution. As the changes that organisms make in their environments can persist for longer than the lifetime of an individual organism, niche construction can generate an extragenetic inheritance in which organisms leave a legacy of modified selection pressures to future generations. Learning and other developmental processes can influence and direct niche construction, and as a result acquired characters can play an evolutionary role.

The joint evolution of environment-altering (niche constructing) traits, and traits whose fitness depends on alterable sources of natural selection in environments are discussed. The evolutionary consequences of niche construction are investigated using a two-locus population genetic model. The novel conclusions are that niche construction can (1) cause evolutionary inertia and momentum, (2) lead to the fixation of otherwise deleterious alleles, (3) support stable polymorphisms where none are expected, (4) eliminate what would otherwise be stable polymorphisms, and (5) influence disequilibrium. The analysis suggest that the changes that organisms bring about in their niche can themselves be an important source of natural selection pressures, and imply that evolution may proceed in cycles of selection and niche construction.

Genetic and demographic factors in extinction

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Deterministic and stochastic factors affecting extinction risk of species or populations will be reviewed in terms of their relative importance and interactions. Genetic factors include inbreeding depression, the accumulation of new deleterious mutations, and the maintenance of genetic variability for adaptive evolution. Demographic factors include demographic and environmental stochasticity, and metapopulation dynamics. The talk will emphasize recent theoretical results on the accumulation of mildly deleterious mutations, and on metapopulations with explicit local dynamics.

Unpredictability of correlated response to selection: linkage and initial frequency also matter

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In a recent paper Gromko (Evolution 49:685-693) showed, using computer simulations, that pleiotropy and sampling interact to generate variation in correlated response to selection. His simulations demonstrated that different combinations of pleiotropic effects could lead to the same genetic correlation value, yet, so far the population size and correlation value were large enough, result in significantly different variance of correlated responses after ten generations of selection. We extended those results using Alan Roberston's "re-parameterization" of selection processes in finite populations. As for direct selection response, a satisfactory description of the correlated response and its variability can be expressed in terms of *Nih, t/N* and *NL,* where *N* is the effective population size, *i* is the selection intensity in standard units, h^2 is the heritability of the selected and correlated traits, *t* is the number of generations and *L* is the length of the chromosome in map units. For a given number of loci, there exits a *Nih* threshold under which differences between pleiotropic systems will not be detected. For values of *Nih* above this threshold, the higher *Nih* is, the smaller *t/N* needs to be for significant differences in correlated responses between pleiotropic systems to be observed. A large number of loci or tight linkage increases the unpredictability of the correlated response but so far *Nih* is large enough it does not absolutely prevent significant differences between pleiotropic systems to occur. On the other hand, a small initial allele frequency of the favourable allele would tend to cancel the differences between pleiotropic systems, even for large values of *Nih* and *t/N*. Finally, epistasis decreases the overall variability of the correlated response but generally preserves the difference between pleiotropic systems. Thus, Gromko's conclusions on the unpredictability of correlated response due to variable pleiotropy seem fairly robust, at least in the long-term.

Genetic structure of the endangered fish *Valencia hispanica* based on mitochondrial DNA restriction analysis.

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Valencia hispanica is considered as one of the most threatened species in the world by the International Union for Conservation of Nature (IUCN). In fact, it has been catalogued as one of the vertebrate species with a higher risk of extinction.

The present distribution of *Valencia hispanica* is restricted to a very few localities of the Valencia region, in the Mediterranean coast of Spain.

The analysis of genetic variability provides valuable information for the management of endangered taxa. Mitochondrial DNA (mtDNA) has been shown as an ideal marker for this purpose due to its high variability, maternal inheritance and lack of recombination.

MtDNA of 115 individuals representing the current distribution of this species, have been digested with 16 restriction enzymes. Phylogenetic and Population analysis of these data have shown the existence of three significantly differenciated populations. The preservation of these three ESUs (Evolutionary Significant Units) would be essential for long-term conservation of this species.

GROWTH-HETEROZYGOZITY RELATIONSHIP IN OYTERS : NEW EVIDENCE FROM MICROSATELLITE MARKERS

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Relationship between heterozygosity at allozyme loci and fitness-related traits (growth, viability...) has often be reported in bivalve molluscs. Two main hypotheses have been advanced to explain this correlation. First, the "direct dominance" hypothesis suggests that the correlation is caused by dominance or overdominance at the scored loci themselves. The second hypothesis, "associative overdominance", assumes that allozyme are neutral markers of effects caused by other genes with which the allozyme loci are in linkage desequilibrium.

Heterozygosity at neutral loci (such as microsatellites) should not correlate with fitness-related traits under the direct dominance hypothesis, but should under the associative overdominance hypothesis. This approach was studied by analysing a cohort of the flat oyster *Ostrea edulis* L. with 5 allozyme loci and 5 microsatellite markers.

A positive correlation was found between allozyme heterozygosity and growth rate. The results on heterozygosity at microsatellite loci are discussed in the light of the conflicting hypotheses.

How to cope with toxic cyanobacteria? Experiments with the water flea *Daphnia pulex*

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Several experiments were performed to study how *Daphnia* populations respond to the presence of toxic cyanobacteria. The focus was on the interactive effects of toxic cyanobacteria and other environmental factors, clonal differences in sensitivity, changes in the horizontal distribution of *Daphnia* and accumulation of toxins in the food-web.

The main results were as follows; 1) the growth of *Daphnia* populations was reduced by the presence of toxic *Microcystis* as a consequence of delayed maturation, reduced reproduction and increased mortality, 2) temperature affected the sensitivity of *Daphnia* to toxic cyanobacteria, 3) some *Daphnia* clones may escape *Microcystis* by producing more resting eggs, 4) *Daphnia* did not avoid extract prepared from toxic cyanobacteria, 5) no toxin was found in *Chaoborus* larvae preying on *Daphnia* exposed to toxic *Microcystis*, and 6) clonal differences in sensitivity to toxic cyanobacteria suggested replacement of the most sensitive *D. pulex* clones during cyanobacterial blooms.

Evolution of the broad specialized bacteria. Klebsiella as the example.

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Klebsiella pneumoniae is a typical pathogenic bacterium, the cause of hospital infections, especially harmful to children. The possibility of the formation of the virulent forms has been studied using K. planticola closely related to K. pneumoniae in taxonomic tests. Klebsiella pneumoniae strains were taken from the clinical bacteria collection; and K. planticola strains that are nitrogen-fixing were isolated from forest soils. Some soil nitrogen-fixing strains have demonstrated weak toxigenity and were slightly virulent in experiments with laboratory animals. The ability of K. planticola to penetrate into the green plant mass has been established in experiments with sterile plants. It might be one of the ways of animal infection with these bacteria, and this results in selection of the virulent forms. Plasmids were not found in soil strains but the bacteria easily acquired them in the process of conjugations with the clinical strains. This lead to bacterial resistance to many antibiotics.

The data suggest that widely specialized bacteria of the Klebsiella genus adapt and survive both in environment and in the organisms of man and animals. One of the proposed mechanisms of the adaptation is connected with the accumulation of plasmids from host bacteria. Such mechanism of adaptation is due to other genera of Enterobacteriaceae: Enterbacter, Citrobacter and it has been confirmed for Yersinia genus.

The evolution of symbiotic structures: a theoretical framework

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The emergence of new, self-replicating units built from independent subunits lies at the heart of some major steps in the evolution of life. How the transition is achieved is not at all obvious, since it is quite possible for natural selection operating at the level of the subunits to disrupt their integration into the larger unit. It is particularly difficult to see how it can come about in cases where the subunits are genetically unrelated and there is no opportunity for kin selection to take place. Attempts to find evolutionary paths leading to integration of unrelated organisms have usually presupposed that each subunit can provide some benefit to its partner so that the success of one is bound to the success of the other. But it is arguable that a more likely starting point would involve the exploitation of one partner by the other, and it is hard to see how integrated symbiotic units can emerge in this case. Here a theoretical framework is described for the coupled evolution of two symbiotic organisms, in which both resource exchange and vertical transmission are able to evolve from arbitrary initial values. With this framework it is possible to investigate the initial conditions from which merger of lineages can be achieved.

Plant domestication: a stochastic model for understanding the influence of the reproduction mode, gene flow and drift on gene organisation

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Domestication is a useful model for studying evolutionary response to selection of plants with contrasting breeding systems. For many plants, domesticated and wild forms co-exist in sympatry whilst presenting huge morphological differentiation. However only a handful of genes seems to be responsible for this differentiation. In this study, we consider a stochastic model simulating the gene flow between a completely wild population and a population with a low frequency of domesticated alleles that is under cultivation. A genetic map containing 100 loci located on 7 chromosomes of 100cM length was randomly built. Those loci coded for 4 domesticated traits which are necessary for the cultivated phenotype. The questions assessed were the relative influence of the reproduction mode, gene flow and drift on the number of genes involved in the domestication syndrome and on their organisation on chromosomes. This model confirms the largely assumed idea that domestication was easier in autogamous plants than in allogamous ones. The results also predict that the number of genes involved in domestication syndrome is larger in autogamous plants than in allogamous ones. Furthermore they show that this process leads to linked combinations of genes in allogamous and dispersed ones in autogamous plants. This model is under experimental validation using the *Gramineae* family. In this family domestication has produced suites of target traits that are often analogous or even homologous among the cultivated species.

Population structures of the clonal grass *Calamagrostis epigejos* in relation to heavy metal stress and habitat heterogeneity

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Clonal plant populations are generally genetically diverse, but a large variation in the level of clonal diversity has been found in different studies.

In four populations of the vegetatively propagating grass *Calamagrostis epigejos* the number of coexisting clones was determined with isozyme markers. In each population 100 individuals were examined. In two populations of unpolluted sites 5 and 10 clones were distinguished, respectively. High levels of clonal diversity were found in the populations of a moderately polluted old sewage farm (59 clones) and of a highly polluted copper smelter (92 clones).

The results demonstrate that clonal diversity can be enhanced in heavy metal stressed populations compared with unpolluted populations. This may be due to different selective regimes. On the one hand, in unpolluted habitats intraspecific competition results in low clonal diversity. On the other hand, stressful conditions decrease the importance of competion and facilitate the coexistence of a great number of clones. Moreover, as metal concentrations were quite heterogeneous, habitat heterogeneity and niche separation may have contributed to increased diversity of the metal contaminated populations.

Analysis of temporal variation in genetic structure between year classes in mediterranean littoral fish, Diplodus sargus

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Marine fish are characterized by a complex life cycle which includes a pelagic larval phase that contrasts with a benthic adult phase in littoral species. This pelagic larval phase and the recruitment stage have been recognised to directly determine the dynamic of population. During these periods, abundance of a year classe can decrease up to more than 99 %. Such a high mortality offers possibilities for selection or/and drift to modify genetic structure of recruited population.

In order to test these hypothesis, we sampled a total of 1153 Diplodus sargus in the area of Banyuls sur Mer (France). Collected fish layed althrough the lenght range to represent a large range of year classes (about 10 years). Each fish was age using image analysis of grounded otolithes to identify year marks. Moreover, we analysed allelic frequencies of 17 polymorphic loci in each fish (Lenfant and Planes, 1996).

Once genetic and age structures were assessed, fish were grouped by year classes. We investigated genetic differences between year classes using Fst data (Slatkin, pers.comm.) and F_k data (Waples, 1989) to estimate effective population size.

Lenfant P. and S. Planes, *Journal of Fish Biology* (1996) **49**, 613-621
Waples R.S., *Genetics* (1989) **121**, 379-391

LENORMAND T.   Sun 24 Aug   S20   T. LENORMAND

Estimating gene flow using selected markers : a case study.

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Estimating gene flow is a major topic in Population Genetics. The common method proceeds through evaluation of genetic population differentiation using neutral markers. Even if such an approach presents the advantage of being applicable in most cases, its main hypothesis -neutrality- is never verified.

Alternatively, we investigate the use of markers evolving under known strong selection pressures taking advantage of this knowledge to estimate gene flow. When this selection is variable in space, it created a genetic differentiation which is swamped by gene flow when selection vanishes. We describe and illustrate the method using data of insecticide resistance genes in the mosquito *Culex pipiens* from southern France.

The evolutionary biology of planetary self-regulation

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There is ample evidence that the Earth's surface environment has been regulated towards comfortable conditions since the origin of life. The central puzzle for evolutionary biologists and geophysiologists is: How does self-regulation arise on the Earth? To help address this puzzle we introduce a classification of the feedbacks between organisms and their environment. Four properties of organisms; growing, altering their environment, experiencing environmental constraints and undergoing natural selection, appear to contribute to self-regulation.

A simple model of biological amplification of rock weathering shows strong system self-regulation without any natural selection. It illustrates that the spread of a trait that alters the environment in a manner that is favourable to growth tends to be reinforced. In contrast, the spread of a trait that is altering the environment away from comfortable conditions is restricted. The Daisyworld model and its descendants demonstrate that natural selection can enhance planetary self-regulation. Indeed, introducing random mutation of daisy colour into a Daisyworld that begins with a grey daisy of the same albedo as the planet's surface, generates regulation.

The daisies of Daisyworld provide an example of what we call 'selective feedback' to describe the effect of traits that, as they spread, alter the forces of selection on themselves. Selective feedback makes a direct connection between the individual level of selection and the larger scale of environmental alteration. Examples from the rainforests and boreal forests illustrate how selective feedback can contribute to the Earth's self-regulation, whilst the implications of dimethylsulphide production by marine phytoplankton offer a rich area of research for evolutionary biologists and geophysiologists together.

Developmental instability in haplodiploid spider mites.

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In mites, pattern and number of leg setae and solenidia are well defined and species-specific. These bilateral traits commonly show discrete (meristic) variations. Random deviations from a perfect bilateral symmetry i.e. fluctuating asymmetry (FA) is considered as a good indicator of developmental stability. In two-spotted spider mites (*Tetranychus urticae*) fertilized eggs give rise to diploid females and unfertilized eggs to haploid males. Fluctuating asymmetry of leg setae and solenidia was investigated in a laboratory strain and in two wild populations of *Tetranychus urticae.* In the laboratory strain, meristic variations of each trait were independent and their heritability was nil. The level of FA was higher in the laboratory strain than in the two wild populations and the variable traits differed from one population to another. In the 3 populations studied, haploid males consistently showed more fluctuating asymmetry than diploid females. The effects of the level of ploidy and heterozygosity on mites developmental stability will be discussed.

Body size evolution and the genetics of growth in *C. elegans*

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We have studied rhabditid nematodes, of which the model organism *C. elegans* is one, in order to identify the precise cellular causes of evolutionary variation in body size (about 15-fold by volume). We have focused on the epidermis, the organ most obviously responsible for growth. The epidermis of a rhabditid nematode is largely a single syncitium that grows as epidermal cells -- the daughters of a set of lateral blast cells -- fuse with it. Evolutionary differences in body size are, at least in part, due to the number of such cells that are produced in the course of development. In other words, cell number matters, and we have studied epidermal cell lineages in great detail in order to identify precisely where divisions are gained and lost in the course of evolution. But much of the evolutionary variation in nematode body size *cannot* be accounted for by variation in cell number: some species having much larger or smaller cells than *C. elegans*. In other organisms, large cells are often associated with multiplication of the genome via germ-line polyploidy or somatic polyploidy (endoreduplication). Epidermal nuclei in *C. elegans* endoreduplicate (becoming 4C by adulthood), and it appears that in nematodes, evolutionary variation in cell size is closely correlated with variation in the ploidy of epidermal nuclei; that is, the degree of endoreduplication varies. Thus we have a hint of how cell size is controlled in the course of evolution. In order to identify candidate genes which might underlie this evolutionary variation, we have started a long-term project to work out the control of body size in *C. elegans* at the molecular level. Numerous body size mutants are known in *C. elegans* including both dwarfism and gigantism loci. Many of these turn out to be cell size mutants. Some have been cloned and are homologous to genes involved in the signal transduction of mammalian growth factors belonging to the TGF-β family. We are also about to start studying recombinant inbred strains whose parents are divergent wild-isolates of *C. elegans* in order to see what kind of genetic variation for body size is segregating in natural populations.

Molecular phylogeny of Salicaceae and closely related Flacourtiaceae: Evidence from 5.8 S, ITS1 and ITS2 of the rDNA

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A ribosomal DNA region, including the 3' end of the 18S RNA gene, the entire 5.8S RNA gene, the 5' end of the 28S RNA gene and the internal transcribed spacers ITS 1 and ITS 2, was used for studying the phylogeny of Salicaceae and the relationship between Salicaceae and Flacourtiaceae. The length of the ITS regions within Salicaceae and Flacourtiaceae was similar to that found in other angiosperms. The variation in length was 215-241 bp in ITS 1, 207-223 bp in ITS 2 and 162-164 bp in the 5.8S rDNA. The GC content of both ITS regions was high, varying between 62.7-71.2%. The interspecific variation in the ITS sequences was very small in the genus *Salix*, which is in contradiction with the age of the group according to the evidence from fossile data. The most parsimonious tree showed Salicaceae as a monophyletic group. The wind-pollinated *Chosenia bracteosa* has been separated from the insect-pollinated genus *Salix*, and it grouped among the *Salix* species, making *Salix* a paraphyletic group. *Populus* was monophyletic and formed a sistergroup to *Salix* and *Chosenia*. Within *Salix*, the species *S. alba*, *S. amygdaloides*, *S. fragilis* and *S. pentandra* formed a subgroup, which partly supports Dorn's division into two subgenera, *Salix* and *Vetrix*. The phylogenetic analysis supports the close relationship of *Idesia polycarpa* (Flacourtiaceae) to Salicaceae, which has earlier been suggested on the bases of other characters.

Prey choice and associated reproductive success of a soil-inhabiting predatory mite

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Based on selection and cross-breeding experiment it was shown that local populations of the predatory mite *Hypoaspis aculeifer* exhibits a genetic polymorphism in prey preferences with respect to two species of astigmatic mites (*Rhizoglyphus robini* and *Tyrophagus putrescentiae*, further referred to as R and T). To investigate whether prey preference reflects reproductive success the population growth of isofemale lines was assessed when reared on an ample supply of each of the two prey species alone or on a mixture. It was found that the R-preferring isofemale line (R-line) increases faster on a diet of R than on T, and that the T-line increases as fast on T as on R. Surprisingly, both the R-line and the T-line performed much worse on the mixture of the two prey, but the T-line did relatively better than the R-line. In simultaneous experiments hybrids always showed a lower growth rate on each of the prey alone than the parental lines, but they performed relatively better than their parents on the prey mixture. Most strikingly, the hybrids with a T mother did much better on the mixed prey diet than the hybrids with an R mother. This suggests that the T-line contains traits coding for better performance on a mixed prey diet.

Parallel to the above experiments with pure lines and their hybrids also the base population was tested, i.e. the field-collected strain that was reared in the lab and that served as "raw material" for the selection experiments. In sharp contrast to the selected lines this strain showed a great potential to increase on each of the prey alone, as well as on the prey mixture. This suggests that the base population contains even more genetic variability, either due to cross-products of the two selected lines or to yet other genotypes. Hence, there is every reason to suspect populations of these predators to exhibit genetic polymorphisms. Whether this picture also applies to other arthropod predator-prey systems, remains to be seen, but if so the consequences for their dynamics will be dramatic.

The population genetics of adaptive evolution in primarily clonal populations of parasites.

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For the most part, the formal (a euphemism for mathematical) theory of the population genetics of adaptive evolution has been developed for free-living, sexually reproducing diploids, like the vast majority of the readers of this abstract. In these organisms, recombination rates are high and associated linkage selection and numerical bottlenecks play relatively minor roles in the process of adaptive evolution. While in sexually reproducing populations with high recombination rates, there are situations where the highest fitness allele at a locus may not ascend in a given population, the conditions for this situation, the best not evolving, to obtain are relatively restrictive. In this talk, I will argue, present models, and even evidence (from studies with rpsL system of E. coli), that indicate that in bacteria and other parasitic organisms that reproduce asexually and in which recombination is rare, associated linkage selection and the bottle necks associated with infectious transmission play a dominant role in the process of adaptive evolution.

As a consequence of these and other phenomena, like host and environmental variation, populations of these clonal reproducing parasites, will remain far from the best they can be and doubtless will be on Equilibrium Day.

Radiation in some subgenera of large carpenter bees in relation to their mating system.

Remko Leijs Presenter: M. Schwarz

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The genus *Xylocopa* (large carpenter bees) consist of 35 subgenera which comprise approximately 750 species. Among other factors, the subgenera differ greatly in their mating systems. In some taxa mating occurs predominantly at sites that contain resources for females (flowers, nesting sites). Males may or may not defend territories in the neighbourhood of such resources. In these subgenera sexual dimorphy is usually not very marked. In other subgenera, males defend non-resource territories (leks). Males of those groups show strong sexual colour dimorphy and have enlarged metasomal glands which produce fragrances to attract females.
The basal subgenera of the genus *Xylocopa* all have resource based mating systems. Lekking seems to be a derived character that has evolved at least three times in the genus. Although mating behaviour has been studied in sufficient detail for a few species only, female choice seems to be more important in lekking species than in non lekking species. This creates a potential for speciation through sexual selection in the lekking species.
In this presentation it is shown that there is a large difference in speciosity between lekking and non-lekking subgenera. It is likely that this difference is due to sexual selection operating more strongly in lekking species. The ways in which female choice and male odour production might be involved in the radiation of some of those subgenera will be discussed.

Visibility and the effectiveness of signaling

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Aposematic individuals are usually very conspicuous and thus very different from the background. Therefore it is assumed that they are more easily detected by predators. There is, however, very little evidence how the visibility of a prey affects the predation and more interestingly what the visibility costs for prey individuals have been in the rising of aposematic forms from the cryptic population. The advantage of being conspicuous is well documented to enhance the avoidance learning and the memorability of the signals by predators. But being too conspicuous at first can also be very dangerous and thus the evolution from crypticity towards aposematic appearance might have been gradual.

Following the logic from Alatalo & Mappes 1996, (Nature 382, 708-710) we created an novel world, where we were able to alter the visibility and thus the visibility risks of the aposematic forms. We used Great tits (*Parus major*) as predators. Although the most visible prey items were digested at higher level at first this led to more stronger aversion learning. But another route from gradual change could also be possible since it did not increase the visibility and thus they experienced the same mortality as cryptic forms but the learning by predators was also very mild. Implications of visibility of the signal in relation to solitary or aggregated lifestyle will also be discussed.

Quantitative variation in selfing *Arabidopsis thaliana* (L.) Heynh. and outcrossing *Arabis petraea* L.

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There is less quantitative genetic variation within selfing plant populations than in outcrossing populations. The mechanisms causing these differences have recently been discussed in theoretical studies (Charlesworth and Charlesworth 1995). Studies on related species with different mating systems are needed to examine the effect of mating system on quantitative genetic variation and how the variation is maintained.

Arabidopsis thaliana (L.) Heynh. and *Arabis petraea* L. (incl. *Arabis lyrata*) are closely related selfing and outcrossing species, respectively. We are examining quantitative variability in these species. The amount of phenotypic variation between and within populations is studied in a common garden experiment. The components of genetic variation within populations are studied with a diallel design. The quantitative characters studied are timing of flowering and leaf morphology. Here we present the results of the common garden experiment. The study was initiated at summer 1996. The *A. thaliana* populations studied then are Nurmes and Naantali (Finland), a Danish population and Limburg (Germany). The studied *A. petraea* populations are from Iceland, Karhumäki (Russia) and Mjällom (Sweden).

Seasonality of births in *Homo sapiens* in pre-industrial Finland: maximisation of offspring survivorship?

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We examined the seasonal variation in human birth and infant survival rates in pre-modern Finland. If survival probabilities of children born during different seasons of the year differ and if timing of reproduction has been affected by natural selection, periodic variation in environment could have led to reproduction during the season of best infant survival expectations. Significant seasonal variation in both birth rate and survival probability was found, but the monthly birth and and survival rates of newborn were uncorrelated. Hence, if there was any tendency to maximise the reproductive success, increase in some other component of fitness than the infant survival was probably targeted. The effect of major holidays on birth rate was proved to be notable, suggesting that although the basis for seasonal variation in birth rate was biological, sociocultural factors have an impact on the timing of reproduction in humans. The overall mortality of infant boys exceeded that of infant girls in all seasons. This difference was smallest during the time of best food supplies, indicating that the development of males was less buffered against environmental disturbances than that of females.

When to have another baby: wealth inheritance and reproductive decision-making in humans

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In most human societies, the inheritance of wealth is an important part of parental investment. Patterns of wealth inheritance and other reproductive decisions, such as family size, would be expected to influence each other. Here I present an adaptive model of human reproductive decision-making, using a state-dependent dynamic model. Two decisions made by parents are considered: when to have another baby, and thus the pattern of reproduction through life, and how to allocate resources between children at the end of the parents' life. Optimal decision rules are those that maximise number of grandchildren. The dynamics of the model are based on a traditional, African, pastoralist system, against which the predictions of the model are tested empirically. High fertility and a biasing of wealth inheritance to a small number of children are frequently optimal.

Most such societies are now undergoing a transition to lower fertility, known as the demographic transition. The model is used to predict which variables would predict such a demographic transition. The effects on fertility and wealth inheritance strategies of reducing mortality risks, reducing the unpredictability of the environment, and increasing the costs of raising children are explored. Reducing mortality has little effect on completed family sizes of living children or on the wealth they inherit. Increasing the costs of raising children decreases optimal fertility and increases the inheritance left to each child at each level of wealth, and has the potential to reduce fertility to very low levels. Reasons why wealth and reproductive success appear to be de-coupled in modern societies are discussed.

Genetic relationships between virulence and transmissibility in malaria parasites

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A rapidly expanding body of evolutionary theory addresses how natural selection might determine parasite virulence. However, relevant experimental data are extremely limited, especially in hosts with sophisticated immune responses. We have used the rodent malaria (*Plasmodium chabaudi*) in laboratory mice to measure the genetic relationship between virulence (measured by initial parasite replication rates, and by mouse body weight loss) and transmissibility (measured by the number of sexual forms of the parasite in the host, and by infectivity to mosquitoes). Based on preliminary results, it appears that virulence is strongly positively genetically related to transmissibility at low levels of virulence but that at higher levels of virulence this relationship flattens out. Thus the data support the prediction that virulence evolves to an intermediate level in order to maximise transmission.

MAKARIEVA A.M.   Sun 24 Aug   S24   A.M. MAKARIEVA

Can evolution be explained without horizontal gene transfer?

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Under natural conditions accumulation of deleterious mutations in a population is limited by natural environmental selective pressure and process of competitive interaction of individuals inside the population, normal wild-type individuals being favoured. In a destroyed environment this mechanism of preventing species genome from decay does not function properly and there may accumulate individuals carrying a great number of deleterious mutations - up to the lethal threshold. Thus there appears a tail of genotypes with decay mutations surrounding the previous normal wild-type genome (these decay genotypes will be again eliminated after the population returns to its natural environment).

It is usually believed that among these generally decay genotypes may be found one that will be able to serve as a wild-type genome of a new species, i.e. this particular genotype will carry one or more progressive mutations. Due to the universal biochemical organisation of genomes of all species, it is natural to expect that the proportion of progressive mutations in the total number of mutations should remain more or less constant for all species. Rate of accumulation of mutations in a population is proportional to population number divided by generation time and differs by 15-20 orders of magnitude between procaryotes and eucaryotes. Procaryotes should then evolve 15-20 orders of magnitude faster than eucaryotes, which is in strong contradiction with the observed data.

A possible solution is horizontal gene transfer. Viruses and bacteria live in huge populations and possess short generation times. It makes them possible during short periods of time to generate new progressive fragments, which can then be transmitted to eucaryotes via unilateral horizontal gene transfer. The observed absence of transitional forms between evolved species also finds its explanation - formation of a species appears as a sudden jump from one wild-type genome to another with subsequent relatively rapid "tuning" which results in that the observed genetic differences between closely-related species are dispersed over the whole genome. The unique genetic fragment(s) which initiated the process of speciation may remain unnoticed due to their relatively small length.

We here discuss in detail the proposed conception.

mtDNA polymorphism as a marker of *Phytophthora infestans (Mont.) de Bary* populations reorganization on territory of Russia in the 1990's.

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The mitochondrial DNA polymorphism analysis of 176 *P.infestans* strains, collected in 1990-95 in Russia, has demonstrated reorganization of the plant pathogen populations. As well as in Europe in the late 1970's, in Russia the "old" strains with Ib mitochondrial type present in 1991 and previous years have been replaced by "new" strains with Ia and IIa mtDNA types. In comparison with potato in tomato populations such replacement are late. The partial genetic isolation between *P.infestans* populations on potato and tomato plants is probably supported by existence of own tomato strains inoculum sources outside of stored potato tubers.

The isozyme analysis has not found out of recombination between "old" and "new" genotypes. That confirms a hypothesis about existence an uniform, closely related and sexually isolated group of "old" strains *P.infestans* with Ib type mtDNA (Carter et al., 1990).

The amplified by PCR P2 fragments of three different mtDNA types (Ia, Ib and IIa denoted under the Bangor system; Carter et al., 1990) have been sequenced. It was shown that a samesense-mutation of the Msp-site presented in a region, encoding the ATPase-α subunit, and missense-mutation of the Msp-site presented in an encoding the NADH dehydrogenase subunit 4 region, resulting to replacement of threonine by proline in *P.infestans* strains with Ib mtDNA.

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MAPPES T. Thu 28 Aug C5 T. MAPPES

Negative phenotypic and genetic correlation between litter size and offspring quality: optimal prenatal effort in the bank vole

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One of the main assumptions of life-history theory is the trade-off between the number and quality of offspring. However, the evolutionary basis of this trade-off is poorly tested in free-ranging animals. We studied the prenatal reproductive effort of bank vole *Clethrionomys glareolus* females in laboratory, outdoor enclosures and free-ranging populations. We found significant negative phenotypic correlation between number and size of offspring at birth in all three environments. Further, increasing of litter sizes by hormonal manipulation simultaneously decreased the offspring size at birth. Size at birth correlated positively with future survival and breeding success of offspring. Mothers seemed to allocate between litter and offspring size in the way that maximizes the number of recruits. Finally, the negative genetic correlation between the number and size of offspring demonstrated that the trade-off is under genetic control and so evolutionary meaningful.

The role of secondary plant compounds in defense against pathogenic fungi: costs and benefits of iridoid glycosides.

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Secondary plant compounds can play an important role in the survival of plants under natural conditions. They can act as defence chemicals against herbivores and pathogens. Iridoid glycosides are monoterpene derivates which are produced in the lipid biosynthesis pathway. They can occur in two forms: a glycone moiety, generally deterrent to generalist herbivores, and an aglycone moiety (the product of enzymatic conversion of the glycone moiety with a specific ß-glucosidase enzyme) often with antimicrobial activity. *Plantago lanceolata* produces the iridoid glucosides aucubin and catalpol, which can constitute up to more than 10% the dry weight of reproductive tissues. They are deterrent to generalist herbivores. In this project we study benefits and costs of iridoid glycosides in *P. lanceolata* and their role in defence against a phytopathogenic fungus *Diaporthe adunca*.

An inoculation experiment was performed to investigate the response of plant iridoid glycosides to fungal infection. The results showed that constitutive levels of iridoid glycosides amounted up to ca. 6% of the dry weight of scapes and ca. 4% of the dry weight of spikes. There was a highly significant induction of iridoid glycosides in reproductive tissues (where infection takes place) which occurred very soon after inoculation (< 6hrs). The level of induction was higher in the spikes and scapes of the resistant genotype than those of the susceptible genotype, whereas constitutive levels were higher in the susceptible genotype than in the resistant genotype.

In vitro, addition of the aglycone moiety of both aucubin and catalpol to liquid growth medium of the fungus *D. adunca* reduced the growth of the fungus compared to the control ($P<0.001$). But the addition of the glycone moiety of aucubin induced fungal growth compared to the control ($P<0.001$) whereas catalpol had no effect on fungal growth.

Growth response to a salinity gradient on microscopic stages of an intertidal kelp: A reaction norm approach.

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The estuary of Con-Con river, in the central coast of Chile, is one of the few having rocky shores, instead of large sandy beaches on the riversides that reach the sea. *Lessonia nigrescens* Bory is an intertidal kelp that have an haplo-diploid type of life history, with microscopic dioic gametophytes which, after fertilisation, give raise to the large sporophytic phase. This phase becomes mature after 2 years. The presence of sporophytic individuals is almost constant along the 4200 km of the chilean Pacific coast, where salinity is normally over 30‰. However, within the estuary of Con-Con this kelp was present even on those rocky riversides where daily salinity variations descended to 20‰. The question addressed in this study was whether the presence of this kelp in this low salinity site might imply inherited capacities of resistance to this environment. Then, the growth response of the microscopic offspring was compared between descendants of plants attached to both extremes of the salinity gradient. For this, on a common garden experiment under laboratory conditions, growth was measured for microscopic plantules submitted to a salinity gradient from 16‰ to 32‰.

After 40 days of incubation, the microscopic sporophyte progeny of adult plants from both extremes of the salinity gradient showed the lowest growth at 16 ‰, with mean plantule lengths ranging between 200 µm and 300 µm. The highest sizes were obtained at normal salinity (32 ‰), with mean values ranging between 600 µm and 700 µm, in the same incubation period. However, the positive linear relationship ($Y = a + bX$) between salinity (X) and growth (Y) had a significant steeper slope ($P<0.05$) for plants coming from the site with natural salinity than for those coming from the site with the lowest salinity. This difference in slopes of the reaction norms implies that offspring growth was higher where the salinity of the incubation medium and that of the natural environment of their parental plants were more similar. The genetic structure associated to this subpopulation differences remains to be investigated.

Evolutionary branching and coexistence of germination strategies

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In unpredictably varying environments mixed strategies are among the best devices to maximise the long term growth rate of the population. For example, delayed germination is often detected in annual plants living in risky environments mainly in early successional phases. The seeds of these plants use a mixed strategy as a risk spreading mechanism in time.

We studied the evolution of germination rate using a newly developed theoretical framework (Metz et al. 1995, Geritz et al. 1997) based on the ESS theory, which is constructed for modelling evolutionary dynamics with frequency dependent selection. In spatially heterogeneous and randomly varying environments the germination strategy may undergo evolutionary branching.

As a result, two of these mixed strategies can coexist in an evolutionarily stable coalition, instead of one common mixed strategy inhabiting the population. Since spatial heterogeneity and restricted migration are required for evolutionary branching, the development of polymorphism can be regarded as parapatric speciation. Moreover, population dynamical instability may lead to cyclical evolutionary branching and extinction of a germination strategy.

Testing general theories of senescence: evolution of G-matrices and mean values of life history traits during the adaptation to a novel environment

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There are several hypotheses to explain senescence - developmental theory, unitary hypothesis, antagonistic pleiotropy (*e.g.* costs of reproduction), accumulation of mutations - leading to different predictions about the association and genetic variability of several life history traits. Empirical studies have given contradictory results, some of which may be related to the fact that the populations were far or close to genetic equilibrium. The analysis of the evolution of genetic parameters may also be of value in the detection of mechanisms with little genetic variability at advanced generations and to test the hypothesis of accumulation of mutations. It will also be interesting to analyse evolutionary changes of mean values of several traits, *e.g.* starvation resistances may help to discriminate between costs and risks of reproduction.
We made a genetic study of a population of *Drosophila subobscura*, analysing half-sib samples till generation 29 since foundation to the lab. The traits were early and late fecundities, longevities and time of development. We did also a temporal comparative analysis, involving starvation resistance, between a population already stabilized in lab and a new one. We obtained indications in favour of reproductive costs and accumulation of mutations, both related to the evolutionary theory of senescence. Far from genetic equilibrium we had indications of mechanisms related to the unitary hypothesis and the developmental theory, but they seem irrelevant to the explanation of genetic variability for senescence at advanced generations, contrary to the previously mentioned mechanisms.

Ancient and recent duplication events in *Artemia* provide a model for intron positional stability

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The brine shrimp *Artemia* possesses an unusually large hemoglobin (Hb) formed by two 9-globin polymers in quaternary association. Two different polymers exist, designated T and C which pair to produce either homodimer or heterodimer forms. Sequence analysis of T and C complementary DNA clones reveals that gene duplication has played a significant role in the evolution of *Artemia* Hb. The formation of an ancestral 9-domain Hb from a monomeric primordial Hb by a series of duplication events appears to have occurred at least 700 million years before present. Gene duplication is also thought to be involved in the formation, 60 million years ago, of the precursors of the present day T and C polymers. Thus, two evolutionary periods are present from which to analyse intron stability. Intron movements during the first period from at least 700 million years ago until present were determined by comparison of positions of introns within domains of a given polymer. Intron movements over the second time interval (60 million years ago until present) were determined by comparing intron positions between the T and C polymers. The positions of most of the introns (20 introns per 9-domain gene) in each of the 18 globin domains present a picture of overall positional stability although rare intron movements have been identified.

General Plant Defense Theory: Looking Backward and Forward

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General plant defense theory which has developed exponentially in the last 50 years is reviewed and organized into a "phylogenetic" tree with all of its attendant bushiness. The fundamental arguments about the costs of defense and factors controlling defensive investments are reviewed and challenged. Some of the newest trends in plant defense theory are those arising from the herbivores' potential for manipulation of the plant's developmental bauplan and the plant community for its own gain. McNaughton's grazing lawn concept, and the works of Price et al. on the resource regulation hypothesis, and Haukioja et al. on the induced amelioration hypothesis are compared. Under some circumstances many of these plant/herbivore interactions may be considered part of the extended phenotype hypothesis sensu Dawkins.

McVEAN G. Tue 26 Aug S10 G. McVEAN

Testing the conflict theory of genomic imprinting

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The potential for genetic conflicts within a genome is great. But to what extent has conflict been responsible for shaping genetic systems? One system proposed to be the result of intragenomic conflict is that of genomic imprinting; genes for which expression is dependent upon the parent from which they are derived. However, the conflict theory is but one of a number proposed for the evolution of imprinting. We have therefore examined three predictions of the conflict hypothesis as an empirical means of testing its validity.

First, we have shown that, in accordance with the predictions of the conflict hypothesis, where imprinted genes have an effect on growth, paternally expressed genes tend to be growth promoters and maternally expressed genes growth repressors. There are, however, possible exceptions to this rule. Second, the conflict theory is unique in predicting that antagonistic coevolution, mediated by changes in protein structure, may develop over the control of foetal growth demands. We have examined the evolution of insulin-like growth factor 2 (*Igf2*) and its antagonistic receptor (*Igf2r*) and find that they are highly conserved at sites of mutual binding. In addition, the rate of molecular evolution of seven imprinted genes sequenced in both mouse and rat, is the same as that of non-imprinted receptors and significantly lower than that of immune genes. Finally, we have collated data on the effects of uniparental disomies (UPDs) on foetal size in humans. This provides only partial support for the conflict hypothesis and several clear cases, in direct opposition to its predictions, where paternally inherited UPDs result in small foetus size. The extent to which these findings require revision or rejection of the conflict hypothesis are discussed.

MELSER C. Mon 25 Aug C3 C. MELSER

Does *Echium vulgare* abort seeds selectively?

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Echium vulgare is a biennal, self-compatible species. Each flower contains four ovules, but on average the seed set per flower does not exceed 1.5. The low seed set per flower is not due to insufficient or incompatible pollen, but seems to be caused by abortion of the seeds. Why do plants produce more flowers than would be necessary for their production of seeds? Potentially the surplus of flowers could be used to select embryos with the highest quality. To investigate the selectivity on the paternity of the seeds, pollination experiments were carried out with single donors per flower and with a pollen mixture. The paternity of the seeds resulting from mixed pollinations was investigated employing RAPD marker analysis. All combinations of pollinations set seed, but the pollen donors differed in their amount of seeds sired per flower. Overall, there was no distinction between self- and cross-pollinations. However, some motherplants produced less seeds after self-pollination compared to cross-pollination, while others produced more seeds after selfpollination. Plants that produced more seeds after self-pollination were also more successfull in siring seeds on other plants. These results could be explained by considering the presence of both recessive and additive deleterious alleles.

Geography of quantitative trait divergence in the Greenfinch (*Carduelis chloris*) - comparison to allozymes

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Quantitative trait divergence and variability among 12 greenfinch populations across continental Europe was examined and compared to divergence in neutral genetic markers (allozymes). The added among locality variance component for 16 skeletal traits was large (mean 28%, range 4-48%) equalling a divergence of up to three *SD* units. The divergence in quantitative traits (Q_{ST} = 0.04 - 0.48) greatly exceeded that in allozymes (F_{ST} = 0.01 - 0.07), indicating the differentiation in quantitative traits to be larger than expected by mutation and drift alone. This conclusion was consistent also with results from the multivariate approach of Rogers and Harpending (1983). However, genetic and morphometric distances between populations were positively correlated, even when controlling for the geographic distance separating pairs of populations. In concordance with Bergmann's rule, most traits were strongly and positively correlated with latitude, indicating latitudinally ordered genetic or/and environmental effects. However, the correlation between lower mandible width and latitude was strongly negative, demonstrating an inverse relationship between beak size and body size across the populations. These results are interpreted to reflect the re-colonisation of history of northern Europe (genetic and geographic distances correlated) which has been parallelled by selection acting on quantitative traits ($Q_{ST} > F_{ST}$). In particular, the counter-gradient variation in beak width, a functionally important trait, is suggestive of an adaptive basis for quantitative trait divergence.

Historical demography of the greenfinch, *Carduelis chloris* - An analysis of mtDNA control-region sequences

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Genetic variability within and among 10 geographically distinct populations of Greenfinche was assayed by directly sequencing a 637 bp part of the mtDNA control region from 194 individuals. 13 variable positions defined 18 haplotypes with a maximum sequence divergence of 0.8%. Haplotype (h = 0.28 - 0.77) and nucleotide (π = 0.058 - 0.17%) diversities within populations were low, and decreased with increasing latitude (h:r_s = - 0.81; π: r_s = - 0.89). The distribution of pairwise nucleotide differences fit better with expectations of a "sudden expansion" than of an "equilibrium" model, and the estimates of long term effective population sizes were considerably lower than current census estimates, especially in northern European samples. Selection is an unlikely cause of observed patterns because (1) the distribution of variability conformed to expectations of neutral infinite alleles model, and (2) haplotype diversity across populations was positively correlated with heterozygosity (H_E) in nuclear genes (r_s = 0.74, $P < 0.05$). Hence, a recent bottleneck, followed by serial bottlenecking during the process of post-Pleistocene re-colonization of northern Europe provide a plausible explanation for the low genetic diversity in the north. Genetic distances among populations showed a clear pattern of isolation-by-distance, and 14% of the haplotypic variation was among populations, the rest being distributed among individuals within populations. In accordance with allozyme and morphological data, a hierarchical analysis of nucleotide diversity recognized southern European populations as distinct from northern European ones. However, the magnitude of divergence in mtDNA, allozymes and morphology were highly dissimilar (morphology > mtDNA > allozymes).

Origin of the association of a lethal gene with the O_5 chromosomal inversion in colonizing populations of *Drosophila subobscura*

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D.subobscura, a typically Palaearctic species, has recently colonized the American continent. A complete association between a lethal gene and the O_5 chromosomal inversion has been detected in the colonizing populations. Three hypotheses on the origin of this association are analyzed and their probabilities are calculated.

According to the first hypothesis, an O_5 chromosome carrying a lethal gene would have been included in the sample from which the colonization started. The calculations show that this hypotesis is the most likely. Thus, if a Palaearctic population was found to carry the lethal gene on an O_5 chromosome, this would be a candidate for the population from which the colonization started, but such a population has not been found.

MICHALAK P.. Wed 27 Aug S5 P. MICHALAK

Tests for sexual isolation between two newt species, *Triturus vulgaris* and *T. montandoni*

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Homo- and heterospecific crosses between the smooth newt, *Triturus vulgaris*, and Montandon's newt, *T. montandoni*, were staged in order to identify behavioral basis of sexual isolation. Courtship encounters deliberately involved only one female and one male to eliminate the potentially confounding effects of male-male competition and variation in mate encounter rate. Our experiment revealed significant variation in mating parameters calculated separately for three different courtship phases (distinguishable by the onset of display, spermatophore deposition and its transfer). We found significant differences between crosses for both mating success and duration of the courtship phases. Only 4% of all heterospecific encounters progressed to successful spermatophore transfer (in contrast to 34% of homospecific ones), thus producing high values of sexual isolation indices. No significant difference in mating propensity was found. The pattern of difference in the duration of courtship stages will be discussed in the context of two models of asymmetric sexual isolation. Also, we will compare the pattern with our results obtained from other experiments (e.g. multiple mate choice design).

Contrasting diversification patterns between sister clades *Lavigeria* and *Nassopsidia* (Gastropoda:Thiaridae) from Lake Tanganyika: DNA sequence variation and morphology

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The relationship between genetic and morphological diversification is a central issue for a range of evolutionary issues from understanding character evolution, to mechanisms of divergence, to the utility of the fossils in evolutionary studies. Thiarid gastropods in the genera *Lavigeria* and *Nassopsidia* from Lake Tanganyika. East Africa, provide a model system for examining many classic questions about endemic diversification in rift lakes. Earlier work on this gastropod species flock (formerly considered monogeneric in *Lavigeria*) demonstrated clear morphological, anatomical and allozyme divergence among species which share sympartic distributions and common ancestry. My current work compares sequence variation in protein-coding (ND1, Cytb and CO1) and ribosomal (16s) mitochondrial genes and the nuclear ITS2 region. The phylogenetically informative regions indicate that this clade is divided into two sister clades, each with different patterns of molecular divergence. In *Nassopsidia* the OTUs are distinguished by more unique haplotypes and thus deeper branches between taxa, while species in *Lavigeria* present a complex picture of some shared haplotypes and thus shallower branches in the reconstructed phylogeny. It is proposed that this is a result of retained ancestral polymorphisms, possible hybridization and/or recent cladogenesis of *Lavigeria*. *Nassopsidia* species are oviparous with less morphological diversity between OTUs. The *Lavigeria* clade is ovoviviparous and exhibits high levels of morphological diversity. I will compare tests of speciation mechanisms for this molluscan radiation with results from cichlid fish species flocks from the same lake.

MICHOD R. Wed 27 Aug S25 R. MICHOD

Evolution of individuality

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The evolution of multicellular organisms is the premier example of the integration of lower levels into a single, higher-level individual. Explaining the transition from single cells to multicellular organisms is a major challenge for evolutionary theory. In this paper I provide an explicit two locus genetic framework for understanding this transition in terms of the increase of cooperation among cells and the regulation of conflict within the emerging organism. Heritability of fitness and individuality at the new level emerge as a result of the evolution of organismal functions that restrict the opportunity for conflict within and ensure cooperation among cells. Conflict leads—through the evolution of adaptations that reduce it—to greater individuality and harmony for the organism.

Sex-determining mechanisms and the development of the dominant gonad in mammals and birds

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The task of sex determination is to separate potential hermaphrodites into male and female individuals, but the wide variety of sex-determining mechanisms is concerned with a different scenario, namely the developmen relationship of male and female gonads. Mammals and birds are characterized by the contrasting mechanisms of XY male and ZW female heterogamety, respectively, and these, in turn, are related to the sex of the dominant gonad. The dominant embryonic gonad - testis in mammals and ovary in birds - secretes one or more morphogenetic substances that exert a major effect on the sexual phenotype of the embryo. When deprived of their gonads, mammalian embryos develop as females, while avian embryos assume a predominantly male phenotype. In order to fulfil their task of masculinizing the reproductive tract, mammalian testes grow and differentiate faster than ovaries from the beginning of their formation onwards. In birds, the pattern of gonadal differentiation is less straightforward. In chick embryos aged 5 days, male gonads are more advanced than female gonads, as in mammals, but from age 7 days onwards, the ovary has overtaken its male counterparts in size, protein and DNA contents. It is suggested that the male embryo of mammals, developing inside the oestrogen-rich environment of the uterus, may need an active Y chromosome and accelerated growth, in order to enable it to produce male sex hormones from a very early age, whereas the avian embryo, developing outside its mother, may benefit from female heterogamety and early oestrogen production.

Geophilomorph centipedes as a model for the study of segmentation

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Segmental or modular organisation, while primarily a way to increase in size, may also develop functional value per se, thus giving rise to larger occupation of morphospace which, however, is likely to be constrained by the very processes originating segments or modules. Comparative studies within a group of segmented or modular organisms may thus help understanding the underlying morphogenetic processes.

Geophilomorph centipedes are conspicuously segmented animals. Six segments apparently contribute to form the head, which is followed by a long trunk. The number of the leg-bearing segments ($29 \leq N \leq 191$) is variable both intra- and interspecifically. N is always odd and may be equal in the two sexes, or not (difference between sexes thus generally being 2^m, with m integer, often m=1). Species with very high number of segments may belong to derived rather than primitive clades. The full complement of segments is present at hatching, while the post-embryonic development is eventless as for segmental patterns.

Comparative morphological evidence suggests the following model of segmentation: (a) a small number of primary units (eosegments) are specified very early, probably under control from both anterior and posterior terminus; (b) these units undergo a small number (possibly, no more than 5) of doubling cycles; the extent of possible anterior or posterior truncation of the segmental series undergoing individual doubling events being variable, but under strict genetic control, including a very early (embryonic) expression of sexual dimorphism; (c) a last doubling cycle, extending (at least) over the leg-bearing trunk this event being extremely strictly controlled and seemingly autonomous.

Positional information for morphological traits along the trunk is specified by the relative distance from the body ends rather than by the ordinal segmental identity. This seems to reveal the translation of a continuous morphogenetic signal into a discrete morphological arrangement.

Pollen aperture number heteromorphism : the problem of the origin

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Pollen grains of flowering plants are very simple organisms (two or three cells embedded in a highly resistant wall) but exhibit numerous morphological characters susceptible to vary. This variability is well known at all taxonomic levels (from sub-class to species level) and it may also occur within an individual, phenomenon called heteromorphism. Depending on the character which distinguish pollen forms produced by the same plant, heteromorphism will not have certainly the same evolutionary value, variations in pollen size for example may result in differences in germination abilities whereas length variations in the length of the pollen wall prickles would less effect on the ultimate goal of pollen grains (which is fertilize ovules).

Among characters of pollen grains, the aperture and more precisely the number of apertures on a pollen grain is very interesting. Aperture corresponds to opening in the pollen wall by which pollen tubes grow out to convey male gametes through female tissues. The number of aperture is then involved in pollen survival and germination. Moreover, this phenomenon is largely distributed all over Angiosperms Dicotyledons species (around 37 %) and appears in a wide range of Dicotyledons sub-classes. Such a distribution raises the problem of the origin of this phenomenon.

In order to identify factors that may influence the evolution of pollen heteromorphism, we analyze the distribution of heteromorphism at the genus level in *Campanula* and *Medicago* in conjunction with a comparative study across Angiosperms families.

Parasites, host immune defence, and host sexual selection

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Parasites have been hypothesized to play an important rôle in host sexual selection, but both specific studies of particular host-parasite systems and comparative studies have reached mixed conclusions. Since each host species is simultaneously affected by a large number of different parasite species, and since the intensities of infection with different parasites are not generally positively correlated, it is naive to predict that the expression of any secondary sexual character should be negatively associated with a randomly chosen parasite. Since it is unlikely that the same category of parasites (for example Haematozoa) should have the largest detrimental effects on the fitness of all host species, comparative studies of host sexual selection and parasitism are therefore also based on weak and untested assumptions. Host immune systems have been shaped during evolution by the overall impact of parasites on host fitness, and measures of host immune function are much more likely to reveal correlations with the expression of secondary sexual characters than the abundance of a particular parasite. In accordance with this prediction, a meta-analysis of the literature revealed that, while there was no overall effect of parasites on host sexual selection, there was an effect of host immune function. In conclusion, parasites may play an important role in host sexual selection, but the identification of the most important parasite species will invariably be very difficult. Studies of host immune function may provide a better avenue for improved understanding of the rôle of parasites in host sexual selection.

The evolution of endosymbiosis in aphids

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Endosymbiosis has been proposed as an evolutionary innovation that promotes the success and diversification of hosts by enabling them to exploit new ecological niches. In the past decade, our knowledge of the evolutionary history of insect endosymbioses has increased dramatically as a result of molecular phylogenetic studies of a variety of taxa with maternally inherited, bacteriocyte-associated symbionts. It now appears that ancient infection of a common ancestor of a group, followed by parallel diversification of host and symbiont are typical. Molecular phylogenetic studies have provided evidence for ancient infection and cospeciation for endosymbioses of aphids, whiteflies, mealybugs, cockroaches, tsetse flies, and carpenter ants.

Studies of the molecular basis of amino acid biosynthesis in *Buchnera* (aphid endosymbionts) indicate that these bacteria are adapted to provision their hosts with limiting nutrients. Thus, natural selection among host lineages can lead to modifications of the symbionts. Although *Buchnera* has evolved to better serve hosts, they have not acquired genetic features of organelles (mitochondria or chloroplasts), despite at least 150 million years of endosymbiotic existence.

The view of endosymbiosis as an evolutionary innovation conferring ecological advantages to hosts is generally supported by recent findings. However, dependence on endosymbiosis can also be deleterious to hosts in the long run. Molecular evidence for *Buchnera* suggests two processes that might cause endosymbiosis to evolve to the detriment of hosts and the long term detriment of endosymbionts themselves. First, "selfish" mutants among endosymbionts can increase in frequency despite negative consequences to hosts. Second, the small effective population size of endosymbionts combined with their asexuality may cause them to accumulate loads of slightly deleterious mutations. Several lines of evidence for the latter process are presented.

Evolution of metabolic pathways: the histidine paradigm

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The histidine biosynthetic pathway, one of the best characterized anabolic routes, plays a fundamental role in cellular metabolism and it is interconnected to both *de novo* synthesis of purines and nitrogen metabolism. It was one of the metabolic abilities of the last universal common ancestor (LUCA) of the three primary domains (Bacteria, Archaea, Eucarya) and was built in the early stages of molecular and cellular evolution. The comparative analysis of about 100 *his* genes indicates that their structure and/or organization underwent major rearrangements during evolution. In fact the *his* genes **organization** is different in the three domains: in Archaea and Eucarya the *his* genes are scattered throughout the chromosome(s), whereas in Bacteria the organization ranges from a single compact operon (*Escherichia coli, Haemophilus influenzae, Lactococcus lactis*) to separated genes (*Synechocystis*). **Structural changes** involved several *his* genes and include **gene fusion** (*hisB*, *hisIE*) leading to genes coding for bi-or multifunctional enzymes, **gene elongation** (*hisA*) and **paralogous duplication** (*hisH*, *hisA*, and *hisF*). We have reconstructed the evolutionary history of the paralogous genes *hisA* and *hisF* and other related genes which share the same two-module internal organization. These genes are very likely the descendants of a smaller ancestral gene (module *hisA1*) half the size of the present day *hisA* gene and encoding a less specific enzyme able to catalyze two (or more) sequential steps of histidine biosynthesis, in agreement with the **patchwork hypothesis**. This module underwent a gene elongation event leading to the ancestral *hisA* gene which in turn duplicated (before the appearance of the LUCA) giving the *hisF* gene. Then the two genes (*hisA* and *hisF*) duplicated again leading to other paralogous genes with different function.

On the basis of the available data we suggest that the LUCA contained the entire histidine biosynthetic pathway with genes scattered on the ancestral chromosome(s) and encoding monofunctional enzymes.

Genetics of phenotypic plasticity: body size in Drosophila

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Genetic latitudinal clines for body size are known in several Drosophila species, and size decreases according to increasing temperature. Body size is also a plastic trait which exhibits a general trend to decrease at higher temperature. The parallelism between plasticity and clines is an argument for an adaptive change of size, even if we do not know why it is better to be smaller in a warmer environment. The reaction norms of size characters, when investigated on a complete thermal range, are however non linear but convex with a maximum at low or medium temperature. Such a shape can be described by polynomials of 2nd, 3rd, or 4th degree. For each trait (e.g. wing length, thorax length, or ovariole number), the norm can be characterized by the maximum value (MV) and the temperature of that maximum (TMV). Slight but significant differences in TMVs are observed between temperate and tropical populations of *D. melanogaster* and *D. simulans*. More important variations are found between distantly related species adapted to different climates. All the data are coherent: the position of the maximum value is correlated to the thermal niche. More precisely, TMVs are observed at higher temperature in warm adapted populations and species, and vice-versa.

Ref: * J.P. Morin, B. Moreteau, G. Pétavy, A.G. Imasheva and J.R. David. 1996. Body size and developmental temperature in *Drosophila simulans*: comparison of reaction norms with sympatric *Drosophila melanogaster*. Genetics Selection Evolution 28, 415-436.

* J.P. Morin, B. Moreteau, G. Pétavy, R. Parkash and J.R. David. 1997. Reaction norms of morphological traits in Drosophila: adaptive shape changes in a stenotherm circumtropical species? Evolution (in press).

Evolution of the β-subunit of the F-ATPase complex in free living bacteria and *Buchnera aphidicola*, an aphid endosymbiont

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The establishment of permanent and obligate symbiotic interactions is not an easy evolutionary task. It not only has a genomic conflict between non-cooperative living entities to be overcome, but there is also the need for a subsequent accommodation process. The comparative analysis of phylogenetically related free living and symbiotic bacterial species can provide us a better understanding of the genetic and biological transformations that have been necessary to reach and to maintain the symbiotic status.

We have sequenced part of the β-subunit of the F-ATPase complex of the primary bacterial endosymbiont (i.e. *Buchnera aphidicola*) of fifteen aphid species as well as of putative secondary endosymbionts of three of these aphids.

Our results in part agree with those obtained by Moran (1996, *Proc. Natl. Acad. Sci.* USA 93:2873-2878) on accelerated evolution of endosymbiotic bacteria. Relative rate tests showed a higher evolutionary rate of the endosymbiont branch than free living bacteria. We have also detected a mutation pressure towards a high A+T increase. However, the ratio of synonymous versus non-synonymous substitution rates are not different among free living and endosymbiotic bacteria. Although the Muller's ratchet effect promoted by the cytoplasmic inheritance of the clonal endosymbionts is expected to result in an increment in the number of non-synonymous and detrimental substitutions when compared with free living bacteria, additional hypothesis have to be introduced to explain why genes under similar population dynamics show a different evolutionary behavior.

Signs of the hybrid speciation on the Fundulus heteroclitus (Teleostei; Fundulidae) subspecies boundary.

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The mummichog *Fundulus heteroclitus* is a common estuarine fish, chiefly occupying marshes of the North America from Newfoundland to Florida. Two subspecies, different in egg morphology, spawning site preference, and genetics are recognized (Able and Felley, 1986): *F. h. heteroclitus* is distributed south from northern New Jersey, *F. h. macrolepidotus* occupies marshes north. of NY and also in the upper parts of Chesapeake and Delaware Bays. To characterize the *heteroclitus-macrolepidotus* transitional zone fish were sampled in 38 sites between Tuckerton, NJ, New Haven, CT, and Stony Brook, Long Island, NY. Allozymes were resolved using horizontal starch gel electrophoresis. RFLP analysis of PCR - amplified mitochondrial DNA regulatory region was performed to reveal mtDNA haplotypes. We propose that *F. heteroclitus intermedius ssp.n.*, with intermediate allozyme and morphological phenotypes, but with *macrolepidotus*-type mtDNA inhabits estuaries between the areas of *heteroclitus* and *macrolepidotus*. Sharp concordant clines in allozyme (*Mdh*-A) and mtDNA haplotype frequencies show the present subspecies boundary and indicate a substantial degree of reproductive isolation between races. *F. heteroclitus intermedius* might have arisen from asymmetrical hybridization, and now shows evidence for development of reproductive isolation from both parent species. Our results indicate that *heteroclitus* and *intermedius* subspecies are isolated now by a 5 km long marshless beach area in Northern New Jersey. Slatkin's (1993) isolation by distance analysis indicates than gene flow is highly restricted across this border. A heterozygote deficiency found in *intermedius* / *macrolepidotus* boundary sites on the Hudson and Hackensack rivers indicates that these subspecies also have some degree of reproductive isolation. When genetic data for Long Island populations for over 20 years are compared with morphology and genetics of the fish today, they indicate that *intermedius* has now spread out into the former *macrolepidotus* area on the North shore of Long Island.

Geographical patterns of nuclear and mitochondrial variation in two cryptic *Gammarus* types across a contact zone

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At a contact zone of two closely related taxa effects of both - the marginal distribution of both taxa and the interrelation between these two- coincide. It is expected that the diverse DNA markers will show up these effects differentially.

We sampled populations geographically large-scaled around a contact area of two *Gammarus fossarum* types in Central Europe. Individuals have been genotyped by allozyme electrophoresis and mitochondrial DNA sequencing.

With the western *G. fossarum* type a discontinuous 'isolation by distance' pattern was found with high gene flow estimates and low genetic diversity within a population group near the contact zone. This indicates a recent colonization of the western type in this area probably accompanied by a displacement of the eastern type. The geographical patterns of the mitochondrial DNA however suggest potential effects of introgression. The observed patterns of both markers will be compared with morphological and behavioral variation.

Rapid evolution of agonistic behaviour in mice: searching for the phylogenetic pattern within palaearctic genera *Mus* and *Apodemus*

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We collected data on the mean duration of agonistic behaviour between adult mice under standard neutral cage conditions. Both male-male and female-female dyadic interactions in 6 *Apodemus* and 5 *Mus* species were included. Behaviour exhibited in the test considerably varied between species. There were "peaceful" species as well as those highly "agonistic". Phylogenetic analysis revealed low phylogenetic constraints concerning agonistic behaviour. Moreover, surprising differences were found between male-male interactions in closely related species, e.g., *Apodemus microps* versus *A. flavicollis*, *Mus musculus* versus *M. domesticus*. Female-female interactions were "peaceful" in most species. Howewer, in *Mus macedonicus* and *M. spicilegus* they were highly agonistic and resembled the male-male encounters.

The above results confirm the standard view that species specific level of agonistic behaviour can be a subject of rapid evolutionary change.

MUSTAJARVI K. Wed 27 Aug P14 K. MUSTAJARVI

Genetic structure and diversity in relation to population size and isolation in a perennial plant *Lychnis viscaria* (Caryophyllaceae).

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The amount and distribution of genetic variation and their relationship to population size and degree of isolation were examined in 11 populations of a perennial plant *L. viscaria.* Nine of the populations sampled were small isolated peripheral populations, situated in the northern range of the species, where its abundance has been declining during this century. The three remaining populations situated in the main distribution area of the species. Electrophoretic essay on 17 loci revealed low amount of genetic variation in *L.viscaria.* Six loci (35,3%)were polymorphic in at least one population, while the average was only 2,8%. The mean number of alleles of all populations was 1,3 and the mean expected heterozygosity 0.057. Genetic variation was strongly correlated with population size. There was also more genetic variation in central populations measured as expected heterozygosity (H_{exp}=0.114) than in the peripheral populations (H_{exp}=0.034). Of the total genetic variation detected, 86.7% was due to differences among populations. The mean genetic identity of the populations was rather low (0.95), but no correlation was found between genetic distance and geographic distance. This indicates that populations may be even more isolated than expected by their physical distance, gene flow being highly unlikely and genetic drift playing the prominent role in shaping the genetic composition of populations. The low N_em value (0.33) supports this prediction. Relatively high Fis (0.116) value also suggest that inbreeding is commonly occurring.

As the population genetic theory predicts, the genetic variation in *L. viscaria* populations decreases as the population size declines, probably due to increased inbreeding and genetic drift. Isolation from the main distribution area further enchanges the loss of diversity decreasing levels of gene flow. As a result the survival of populations may be endangered as their ability to adapt to changing environments is diminished and offspring fitness possibly reduced.

Mutualists on the edge, or why are there so few parasites?

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One of the best studied mutualisms is that between the Australian lycaenid butterfly *Jalmenus evagoras* and ants in the genus *Iridomyrmex*. The ants provide protection from predators and parasitoids for the larvae and pupae of the butterfly in exchange for food rewards. However, there is evidence that the butterfly caterpillars and pupae manipulate the behaviour of the ants, leading to higher benefits for the butterfly and higher costs for the ants than are expected. Under some conditions found in the field, this may result in the interaction becoming one of parasitism by the lycaenids on the ants.

Given the apparent selection pressure on mutualistic lycaenids to become parasitic on their ant hosts, it is surprising that so few parasitic lycaenids are known. It is possible that this simply reflects the paucity of detailed studies of lycaenid-ant interactions, but it is more likely that evolution favours the maintenance of mutualistic interactions. In this talk I will present some ideas on why crossing the boundary between mutualism and parasitism may be evolutionarily disadvantageous.

Compared patterns of polymorphism and divergence of nuclear rDNA and mtDNA in mites

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Because different regions of the genome can have different modes of evolution and/or transmission, they can be affected differently by evolutionary forces in natural populations, and thus convey complementary and/or contrasted information about the evolutionary history of the species.

We compared patterns of intraspecific polymorphism and interspecific divergence of two markers with contrasted modes of evolution: the ribosomal second internal transcribed spacer (ITS2), a multicopy gene whose copies evolve in concert, and the mitochondrial Cytochrome Oxydase I (COI), which evolves as a single copy gene. Intraspecific variation was investigated in the spider mite *Tetranychus urticae*, an ubiquitous pest. We found no intraspecific variation of ITS sequences in a world-wide sample of this species, as opposed to substantial mtDNA polymorphism. We show by comparisons of both markers among five species of the same genus that this is not due to a slower evolution of ITS2 sequences, which evolve 2.5 times faster than COI. We discuss the possible factors responsible for this apparent contradiction, including concerted evolution of ITS sequences, the recent colonising history of the species, deduced from mtDNA phylogeographic patterns observed, and the ecology of the polyphagous and cosmopolitan *T. urticae*. We present preliminary data on two other mite species with greater specificity and ecological requirements, which show geographically concordant intraspecific variations for both markers.

Drifting of workers and drones as an evolutionary factor in the honeybee Apis mellifera (L.)

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Drifting of workers and drones requires both a mistake by the individual and the acceptance by the guard bees. The acceptance of new workers has a different quality than the adoption of foreign drones. Drifted workers become integrated nest members, usually loose inclusive fitness and increase the fitness of host colonies. Drifted drones, however, decrease the number of sexual offspring of the host colony and increase the potential sexual offspring of mother colonies (Rinderer et al. 1985). Therefore it seems adaptive if acceptance of workers would be higher than acceptance of drones. Workers (n = 1560, 28 colonies) and drones (n = 447; 14 colonies) from 10 breeding lines were sampled at the performance yard Schwarzenau (Germany) in June 1995 and genotyped using four DNA microsatellites. Individuals who did not share one of the queen's alleles at each locus were considered as drifted bees. Putative mother colonies were determined using corresponding genotypes of drifted individuals and queens leading to the proportion of colony members in host colonies. Acceptance of workers (mean = 5,46±4,87) was significantly lower (p < 0,0001; t-test) than acceptance of drones (mean = 53±24,22%). Significant differences (p < 0,01; ANOVA) for the tested breeding lines indicate that drifting behaviour is affected by genetic variability. We conclude that the proportion of drifted individuals is less dependent upon the acceptance thresholds of host colonies but rather a result of individual orientation errors. Since the underlying mechanisms of drifting seem to be similar (Moritz & Neumann 1996) orientation errors are more likely in drones than in workers unless no active host searching mechanism is involved.

Moritz, R.F.A. & Neumann, P. (1996): Genetic Analysis of the drifting of Drones in *Apis mellifera* Using Multilocus DNA Fingerprinting. Ethology 102, 580-590; Rinderer, T.E. Hellmich, R. Danka, R.G. & Collins, A.M. (1985): Male reproductive parasitism: a factor in the Africanisation of European honey-bee populations. Science 228, 1119-1121

The limitations to what we can learn from geographic surveys of genetic differentiation.

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The use of genetic markers has lead to spectacular advances in our understanding of evolutionary biology, most famously by providing evidence extra pair matings in birds which occurred at a frequency much higher than had been suspected from direct observation.

When it comes to relationships between populations and species there have also been successes but also many studies which produced disappointing or equivocal results. How do we make sure that our next study falls in the more desirable category? I will try to identify the strategies that make the most fruitful use of molecular markers.

One important issue is that the rules of inheritance mean that genetic data are highly correlated, with the result that intuitions about sampling strategy can be wide of the mark. For example, it may seem sensible to collect large samples from each locality in order to determine allele frequencies accurately and to make use of highly polymorphic markers, but for many studies the effort would be better expended in different directions. I will illustrate the promises and pitfalls with examples from the study of human evolution.

Analysis of microsatellite DNA from old scale samples of Atlantic salmon (*Salmo salar* L): A comparison of genetic composition over 75 years.

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We studied a Danish population of Atlantic salmon, which has decreased dramatically in size during the last century. There has been some doubt as to whether the original population has gone extinct and, subsequently, the present population has been founded by immigrants. To obtain genetic data from before any severe reduction in population size took place, we extracted DNA from scale samples collected in 1913, during the 1930's and during the 1950's. Using six microsatellite loci, we compared the genetic composition of the "old" salmon population with genetic data from 1989 and data from the closest neighbouring population and another reference population.

Allele frequencies had changed over time, but individuals from recent sample still showed a clear resemblance to the old samples. However, fewer alleles were detected in the recent sample, either due to a population bottleneck or to sampling artefacts.

NIELSEN R. Wed 27 Aug S16 R. NIELSEN

MAXIMU LIKELIHOOD ESTIMATION OF POPULATION DIVERGENCE TIMES

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In this paper we present a method for estimating population divergence times by maximum likelihood in models without mutation. The maximum likelihood estimator is compared to the commonly applied estimator based on Wright's F_{st} statistic. We demonstrate by extensive simulation studies that the maximum likelihood estimator performs several times better in terms of mean square error in most of the parameter range than the F_{st} based estimator. This suggests that in cases where the divergence time is so short that mutations may be ignored, the maximum likelihood estimator should be preferred over the F_{st} based estimator.

Instability of the sexual continuum

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Maynard-Smith and Szathmary (1995) have noted the lack of a model which explicitly demonstrates the instability of a continuum of sexual types with finite interbreeding. To fill this gap, I construct and solve a model which combines nonlinear population-dynamics and quantitative genetics. One can then analyse exactly when and how the existence of the conjectured instability (incipient speciation) depends on an Allee-effect, and how the growthrate and typical character-scale of the instability depends on the amount of competition, mating preference, fecundity, Mendelian segregation and mutations, and on the typical character-scales over which these interactions occur.

Having solved the (linearised) problem of the *onset* of instability, I will also illustrate how the model may be solved (either exactly or to good approximation) in the fully *nonlinear* regime. For many reasonable choices of the parameters, one finds well-separated peaks, i.e. quasi-species. The remaining, relatively weak competitive and/or mating interactions between such species can lead to character-displacement and species-packing limits.

Delayed sexual maturity of three-spined sticklebacks (*Gasterosteus aculeatus*) after introduction of fish predators - phenotypic plasticity?

by

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This study describes how the sexual maturity was delayed in a population of threespine sticklebacks (*Gasterosteus aculeatus* L.), after introduction of a predator fish. No or few predators were present in the lake from 1983 to 1985. Trout were introduced into the lake each year from 1985 to 1990. Before the introduction of the predator the population of sticklebacks was dense. The introduction of the predator caused a decrease in the abundance of the sticklebacks. The introduced trout preyed selectively upon small sticlebacks (one year old). A significantly larger percentage of the sticlebacks became sexual mature at an age of one year, before compared to after the trout were introduced. This delayed sexual maturity is expected from life-history theory. Phenotypic plasticity and evolution by natural selection are candidate mechanisms to explain the delayed sexual maturity. The changes occurred during only five generations, which indicates that phenotypic plasticity is the most plausible mechanism causing the observed change.

Indirect measures of selection on quantitative traits in hybrid zones

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When ecologically and genetically differentiated taxa hybridise at ecotones after secondary contact, phenotypic clines result. Steeper clines for particular traits indicate stronger trait-specific selection. The comparison between clines in a given transect can therefore be used to pinpoint those traits that are mainly responsible for the fit of each taxon to its respective habitat and for the maintenance of the distinction between the taxa. However, such an analysis is hampered by linkage disequilibria. Concordant clines will in part be due to statistical association among loci in hybrid genomes and thus need not indicate identical selection pressures.

Here we present the results of a cline model that was set up to study the dynamics of trait-specific selection on the one hand and genome-wide disequilibrium on the other hand. What is the minimum difference in the strength of selection on two traits that would result in a measurable difference between the two cline widths? If the transition in the phenotypic optimum occurs in a different place for one trait relative to others, how strong does the selection on this trait have to be to displace the phenotypic cline?

Analytical results were obtained under the assumptions of weak selection and a constant genetic variance across the hybrid zone. They suggest that the differences in trait-specific selection need to be large to cause different cline widths, whereas cline position is a more sensitive indicator of variable selection strengths. We tested these approximations with a simulation model which not only relaxes the above assumptions but also allows for an explicit consideration of the genetic basis of the traits.

We apply our results to data on phenotypic clines in the hybrid zone between the toads *Bombina bombina* and *B. variegeta* and discuss the usefulness of the approach for other hybrid zone studies.

Host-retrotransposon coevolution in *Drosophila*. S. V. Nuzhdin[1,2], E. G. Pasyukova[3,2], D. A. Filatov[3] and A. D. Flavell[4]. 1)Section of Evolution and Ecology, University of California at Davis, Davis, CA 95616, USA, 2) Dept. of Genetics, North Carolina State University, Raleigh, NC 27695, USA, 3) Institute of Molecular Genetics RAS, Moscow 123182, Russia, 4) Dept. of Biochemistry, University of Dundee, Dundee DD1 4HN, Scotland.

Transposable elements (TEs) are DNA sequences capable of multiplying on host chromosomes and are an obligate component of the genomes of all organisms. The evolutionary strategy of TE coexistence with the host genome is relatively simple: TEs increase their own copy numbers by transposition, and natural selection against hosts with greater than average number of TEs decreases TE copy number. TE survival is, thus, based on the exact equilibrium between two dynamic processes. This evolutionary strategy has provided a long term stable coexistence of the TEs and the host genome. The TE-host coevolution during the coexistence may lead TEs to decrease their activity, increase it, or even acquire functions beneficial for the host.

We have described *Drosophila melanogaster* inbred lines in which the *copia* retrotransposon has a high rate of transposition. In the line 2b the rate of *copia* transposition was from 10^{-4} to 10^{-2} per copy per generation for 10 years, while 11 other TE families did not move. Initially the rate of *copia* transposition increased together with *copia* copy number, and as many as 11 transpositions per progeny were found at the peak of *copia* activity. Later on, accumulation of factors suppressing *copia* transposition significantly decreased the transposition rate. *copia* transcription was also enhanced compared to the control line OregonR, in which *copia* is stable. We used these lines to make inferences about host-retrotransposon coevolution determining the effects and positions of host genes modulating *copia* transcription, and transposition rate.

98 recombinant inbred lines were created by crossing the 2b and OregonR lines, and full-sib inbreeding the progeny for 25 generations. *copia* and *roo* positions were scored by *in situ* hybridization in all resulting lines. 92 *roo* copies segregating between parental lines and fixed within parental lines were used as stable molecular markers for mapping quantitative trait loci (QTLs) modifying *copia* activity. The interval mapping analysis revealed that *copia* copy number and the segregation of alleles in three host QTLs accounted for the variability in *copia* activity between the RI lines. QTLs situated in the regions 27B-30D, 48D-57C, and 85F-87E, respectively, accounted for 11, 30, and -10% of the difference in transcription between 2b and OregonR.

Reinforcement in Yellow Wagtail (*Motacilla flava*)

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For half a century, several attempts have been made to explain the phenomenon of non-isolated subspecies through reinforcing interactions between selection for postzygotic isolation and adaptations for prezygotic isolation, i.e. the highly controversial theory of "reinforcement". The foundations of reinforcement have come under close scrutiny and though there is hardly any empirical evidence to support it, the process has been found theoretically plausible under restricted circumstances. Under strong selection against non-assortative matings, it might be an important process, though likely too brief ever to be observed in natural populations. Therefore, searching for relics of reinforcement past, i.e. reproductive character displacement, may prove more worth-while than to look for the process itself.

Because reinforcement is thought to exaggerate phenotypic differentiation between populations in contact, it has been assumed to cause inverse relationships between similarity in secondary sexual traits on the one hand and geographical distance and neutral marker divergence on the other. But this traditional assumption cannot be drawn unambiguously from conditions of strong selection, since the strength of selection is governed, at least to some extent, by geneflow, capable of opposing differentiation instead. Considering this, predictions on reproductive character displacement are drawn and tested on natural populations of the polytypic Yellow Wagtail (*Motacilla flava*) by putting the diverse pattern of secondary sexual traits, i.e. male plumage, in relation to the noticeably parapatric distribution of the subspecies and to mtDNA and microsatellite divergence.

The evolution of plasticity in relation to phylogeny.

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The evolution of phenotypic plasticity may be constrained by historic events. Consequently, height, slope and shape of the reaction norm could be related to phylogeny.

The hoverfly *Eristalis arbustorum* shows plasticity in colour pattern and wing length. When reared at low temperatures a darker and smaller colour patches and longer wings are developed.

The plasticity of these two characters as shown in the field, was determined for the seven most common *Eristalis* species in The Netherlands: *E. arbustorum, E. abusivus, E. nemorum, E. horticola, E. intricarius, E. pertinax* and *E. tenax*. The height, slope and shape of the reaction norms were compared with a phylogeny based on morphological and morphometric characters.

No correlation between reaction norm characteristics of both characters and phylogenetic relations was observed, indicating that the evolution of plasticity in colour pattern and wing length was not constrained by phylogenetic relations.

The Probability of Fixation in Populations of Changing Size

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The rate of adaptive evolution of a population rests to a large extent on the rate of incorporation of beneficial mutations. Even beneficial mutations may, however, be lost from a population since mutant individuals may, by chance, fail to reproduce. We have calculated the probability of fixation of beneficial mutations that occur in populations of changing size. We examine a number of demographic models, including a population whose size changes once, a population experiencing exponential growth or decline, one that is experiencing logistic growth or decline, and a population that fluctuates in size. The results are based on a branching process model, but are shown to be approximate solutions to the diffusion model. Using the diffusion model, the probability of fixation of deleterious alleles can also be determined for populations that are changing in size. The results presented may also be used to estimate the fixation flux, defined as the rate at which beneficial alleles fix within a population. The fixation flux measures the rate of adaptive evolution of a population and depends strongly on changes that occur in population size.

Microsatellites variability in European and North American *Carex limosa*, a model species for clonal plant studies.

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Population genetic structure, gene flow and mating systems in clonal plant species remain relatively unsolved. Genetic studies of clonal variation was limited by lack of variation at allozyme loci. However, new molecular techniques give access to more polymorphic markers such as microsatellites. These markers appeared to be powerfull tools to solve genetic questions for species with reduced allozyme diversity. We started to develop microsatellites for the study of an aquatic clonal plant *Carex limosa* (Cyperaceae). *C. limosa* has a circum-boreal distribution, and occurs mainly in mesotrophic fens or trembling bogs. Our overall objective is to determine the basis for different levels of genetic diversity in different natural populations. The first step of our study has been to develop microstellite markers. We selected a first set of 6 primers that were developped on Canadian plant material in a cooperation between the department of Ecology in Nijmegen and the department of plant biology at McGill university (Montreal, Canada). Promising banding patterns were obtained on European material collected in Poland, Finland and Ireland. Optimization i.e. improvement of extraction procedures, PCR and electrophoresis conditions has presently been performed on both European and Canadian plants. In the present poster, we are presenting the preliminary results obtained. The distribution of variability in two Irish populations is described. Furture research using microsatellites in *C. limosa* is outlined.

RAPD variability within and among uni- and bi-sexual populations of *Stratiotes aloides*, the watersoldier.

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The watersoldier (Stratiotes aloides) is a floating aquatic macrophyte of lakes and ditches with a peaty sediment. While the species is dioecious, for a large part of its range in Western Europe populations are uni-sexual, containing only females. Bi-sexual populations, containing both males and females, are rare. Viable seeds are produced only in these mixed populations.
We investigated the genotypic variation in both uni- and bi-sexual populations, using RAPD markers. The results are discussed with respect to two hypotheses:
1) uni-sexual populations were colonized by a single vegetative propagule, and consequently are monoclonal.
2) bi-sexual populations show higher genotypic variation than uni-sexual populations, as a result of sexual versus asexual propagation.

Senescence and species life span as a product of evolution

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The mathematical model of biologic community consisting from population of organisms and food resource is suggested. It is taken into account, that energy, obtaining by organism with food, expenses then on various kinds of vital activity. It is supposed, that besides the energy expenditures on basel metabolism, active metabolism and reproduction there is energy expenditure on supporting of organism structure.

According to Evolutionary Stable Strategy by Maynard Smith during the competition of non-breeding populations distinguishing by values of attributes, survives only one, which values of attribute provides the maximum to fitness of population, determined as a specific rate of rise of population. These values of atributes are evolutionary optimal values .

The species life span is considered from the point of view of evolutionary optimality. It was shown, that stable state of biologic community is the state, when the change of generations (death of adult individuals and appearance of new-borns) takes place. It was shown that the reliable mechanism, providing the change of generations, is the senescence.

The senescence is represented as a process of increasing with age the energy expenditures on the support of organism structure. Natural (senescensal) death happenes in that moment of age, when energy expenditures on the support of organism structure expenditures on various kinds of vital activity exceed the obtained energy. This value of life span provides the maximum to fitness of population.

It was shown, that there are species, in which the death of adult individuals helps the survival of offsprings. In this case the maximum of fitness of population is provided by death of adult individuals much earlier the senescence. (We can observe this phenomenon looking at the populations of some kinds of salmon.)

Associative overdominance and background selection

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Theoretical studies on the effect of deleterious mutations on variation at a linked neutral loci have given contradicting results. In the early seventies it was found that such selection could help to maintain neutral variation. This was explained by associative overdominance which has also been referred to as the cause for the observed relationship between heterozygosity and fitness. More recent simulation studies have though indicated that the variation at linked loci is actually reduced (by background selection). Analytical studies based on assumptions from the coalescence theory have confirmed these later results. In order to validate these results I have simulated individual genotypes, consisting of diploid chromosomes by varying parameter values of mutations, selection coefficients, recombination and population size, and studied the effect of population structure. My results in brief are that associative overdominance may under certain circumstances override the effect of background selection.

Molecular and morphological evidence for host race formation in *Galerucella nymphaeae* (Coleoptera: Chrysomelidae)

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The waterlily beetle *Galerucella nymphaeae* is a herbivore of *Nymphaea alba* and *Nuphar lutea*, (two aquatics) and also of *Rumex hydrolapathum, Polygonum amphibium* and *Potentilla palustris* (all semi-aquatics). The two forms of *Galerucella* could be so-called host races.
Beetles were collected in the Netherlands on different host plants. The total length and the mandibular width were measured to investigate whether the beetles differ in morphology. The results show that beetles living on the tougher plants (*Nymphaea alba* and *Nuphar lutea*) do have larger mandibels.
To determine whether genetic differences exist between beetles from different hosts, RFLP of the ITS1 region of the genomic DNA was used.
The results of the above mentioned investigations will be presented.

Small but significant benefits of female choosiness in a wolf spider?

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Mechanism with which females are supposed to indirectly assess male quality have been widely tested. The conversation has been mainly whether females gain any indirect benefits by their selective mating and whether these benefits are large enough to cover the costs this behaviour incurs. We tested these questions with the wolf spider *Hygrolycosa rubrofasciata* where males court females by drumming dry leaves with their abdomen thus producing audible drummings. Male drumming activity is a honest signal of male condition reflecting male viability. Females prefer actively drumming males as mates but they do not gain any obvious direct benefits via their choosiness. To study the possible indirect benefits we set up a selection experiment where we mated females with two groups of males; the most actively drumming and the least active males. Growth of the offspring did not differ between offspring of two male groups. In survival there was a slight difference corresponding to a correlated response of 0.12 in standard deviation units. Although this benefit is not very large, in a mating a system like this, where females already by passively responding end up mating with a male of higher than average quality, a difference of this magnitude might be enough to benefit females. By actively selecting males of better quality females might still increase the benefits to their offspring.

Conservation genetics in social insects: indications from a comparison of small and large ant populations

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Despite social insects being extremely numerous and of great importance to the structure of most terrestrial ecosystems, the implications of their social and genetic characteristics for conservation biology has yet received little attention. Compared to non-social insects eusocial Hymenoptera show reduced levels of genetic variation, owing to the fact that only a minor proportion of the individuals reproduces directly. In natural populations of eusocial Hymenoptera we thus expect a positive relationship between the average queen number per colony and the genetic diversity at the population level.

This expectation is tested on data from nine populations of the facultatively polygynous red ant *Myrmica sulcinodis* NYL. from four localities differing in climate and habitat, which were screened for genetic variation at 34 allozyme loci. Two dense and continuous heathland populations in North-West Europe showed a considerable difference in genetically effective queen number per colony. Contrary to our hypothesis, this was not accompanied by a difference in mean heterozygosity. In three highly dispersed mountain populations from the Pyrenees, the estimates of worker relatedness and inbreeding suggest a low queen number and the occurrence of mating within the natal nest. The heterozygosity was less than for the heathland populations.

The low genetic variation in the Pyrenean populations suggests that highly dispersed and fragmented ant populations loose genetic variation through genetic drift. Further, we hypothesise that such loss can be accelerated in a fragmentation–inbreeding syndrome, where population decline is accompanied by mating in the nest and increased load from the production of sterile, diploid males. The general implications for conservation genetics in eusocial Hymenoptera is discussed.

Kin structure is maintained in a seemingly unicolonial ant population having close to zero relatedness among nestmate workers

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The evolution of worker behaviour in social insects is usually understood in terms of kin selection, where some members of a family group forgo their own reproduction for the rearing of relatives. However, several ants species have populations dominating an extended habitat by a high density of socially connected nests, each having multiple reproducing queens. Such 'unicolonial' populations apparently have lost the kin structure of discrete colonies and thus the fitness incentive to reproductive co-operation.

We studied the social and genetic structure in a population of the red ant, *Myrmica sulcinodis* NYL., which had several characteristics of unicoloniality. By using information at nine variable allozyme loci, the genetic relatedness among nestmate workers of the same age was estimated to only 0.058. This value was, however, significantly positive and the genotypic composition of nests differed significantly within nest clusters. More detailed analysis showed that the population was in fact multicolonial and consisted of genetically distinct colonies of 1–4 nests. Thus, quite surprisingly, habitat saturation and the high number of reproducing queens per colony has not led to a total breakdown of kin structure in the population. The factors probably responsible for the maintenance of kin structure are discussed. These include (1) a mixed dispersal strategy of sexuals with mating in the nest beeing common, (2) nest fidelity of queens within colonies, (3) some queens having a disproportional share of the production of new queens, and (4) spatial dynamics of suitable nest sites.

It is suggested that several ant species, believed to have lost colony boundaries within populations, are in fact structured in colonies of related individuals, but that the kin structure has yet gone undetected due to poor resolution of genetical markers. Hence, the occurrence of 'unicoloniality' in social insects may be less paradoxical as is has seemed so far.

Honest information, aggression and olfactory recognition of reproductive status in the queenless ant* *Dinoponera quadriceps

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In ponerine ants lacking morphological queens, intracolonial conflict often takes the form of overt aggression, because all workers have the potential to mate and reproduce. In *D. quadriceps* colonies (82 ± 29 workers, n = 17), one individual has the top rank ("alpha") in a linear dominance hierarchy involving a small number of subordinates. Only alpha mates when foreign males visit the nest, and she monopolizes the production of offspring. Aggressive interactions occur in a highly consistent pattern, indicating that high-ranking nestmates recognize each other's status. After extracting the cuticular hydrocarbons of live ants, we have shown that alpha and sterile ants differ by the relative proportion of 9-hentriacontene. This substance of low volatility is correlated with ovarian activity and appears to be involved in the recognition of reproductive status.

When alpha is experimentally removed, the second-ranking worker ("beta") replaces her. Even in the presence of a mated alpha laying eggs normally, beta continues being aggressive, unlike the other subordinate workers. Indeed, alpha interacts with beta for prolonged periods of time, suggesting that this is needed to prevent alpha's supersedure. When the stakes are high, only the ability to win aggressive encounters gives honest information about the quality of an opponent. For workers lower down the hierarchy however, olfactory communication of status seems appropriate.

Dispersal and the evolution of predator virulence

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Predator-prey systems with predators living for several generations in a prey-patch can be compared with host-parasite systems with parasites exploiting their host. As predators and parasites influence the population dynamics of their victems, evolution of traits that control predation-pressure shows a strong resemblence to the evolution of virulence in host-parasite systems. If predation-pressure is strong (high attack rate, high intrinsic rate of increase of the predators), a prey-patch will be rapidly over-exploited. In order to reduce the local predation-pressure, predators may tune the attack rate ('prudent predation'), but they may also increase their dispersal rate. With regard to dispersal we distinguish two strategies: the 'Milker'-strategy with predators continuously dispersing from a prey-patch, and the 'Killer'-strategy with predators remaining at a patch as long as there are prey available. Milkers – compared to Killers – relieve the prey from predation-pressure and thus allow the prey population to reach a larger size. Theory shows that at the end of the interaction a Milker-population will have a higher number of predators.

In small-scale experiments we have studied the dispersal behaviour of field-collected strains of the predatory mite *Phytoseiulus persimilis*. Although all strains exhibit typically the Killer-strategy, there is some variation concerning the onset of dispersal. At least in one of the strains we have found dispersal of predators far before the moment of over-exploitation of the prey. The consequences for the population dynamics, as well as the evolution of this behaviour will be discussed.

Breeding system and genetic variance in the monogamous, semi-social shrew, Crocidura russula.

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1. The population-genetics consequences of monogamy and male philopatry (a rare breeding system in mammals) were investigated in the semi-social and anthropophilic shrew C.russula with the use of microsatellite markers.
2. Genetic diversity was large (H = 0.813) with significant differentiation among subpopulations (F_{ST} = 5-6%) over a small geographical scale (16 km).
3. Subpopulations were themselves structured into smaller units (« breeding groups ») comprising an estimate of four breeding pairs each.
4. Members of the same breeding groups displayed significant coancestries (F_{LS} = 9-10%), essentially due to strong male kinship: syntopic males were on average related at the half-sib level.
5. Female dispersal among breeding groups was not complete (estimate 39%), and unsufficient to prevent inbreeding.
6. From our results, the breeding strategy of C.russula seems less efficient than classical mammalian systems (polygyny and male dispersal) in disentangling coancestry from inbreeding, but much more so in boosting the effective size of subpopulations, and thereby retaining genetic variance.

Genetic structure of nursing colonies of the noctule bat (*Nyctalus noctula*).

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Both the mating behaviour and philopatry are of prime importance in determining the genetic structure of groups of reproductive animals. In summer, females of most bat species form nursing colonies, in which they give birth to their offspring and raise them without the help of the males. Whereas the philopatry determines the structure of matrilineages whithin and among nursing colonies, the relatedness depends also on the relatedness of the mating partners. This paper presents the results of a study of both aspects in nursing colonies of a migrating bat species, the noctule bat (*Nyctalus noctula*). In this species, capture-recapture surveys have shown that a nursing colony consists of two to three hundred adult females.

First, an analysis of the mtDNA control region was used to study the structure of matrilineages. Three copies of a five to ten fold repeated motif, which length is 81 bp, were sequenced in 51 adult females originating from three German nursing colonies. Among the 26 mtDNA types which were found, only two of them are shared by two or the three colonies: the mtDNA type frequency distributions are clearly differentiated. A comparison of these distributions with theoretical distributions obtained by Monte-Carlo simulation show that the migration rate is about 1% per generation, which confirms the natal philopatry of the females.

Second, the relatedness was assessed by means of 11 microsatellite loci, which expressed 9 to 28 alleles in a sample of five nursing colonies. The average relatedness within these five colonies was 0.001 and no difference in the allele frequencies could be detected among them. These results indicate that the different females of a nursing colony mate with different unrelated males. This confirms the fact that twins in the noctule bat have often different fathers.

PICHL H. Wed 27 Aug P8 H. PICHL

Manipulating parental effort: costs of reproduction in the kittiwake Rissa tridactyla

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The cost of reproduction in kittiwakes were studied from 1995 - 1996 on Hornøy northern Norway by enlarging and decreasing brood sizes of two chicks by one at day 3 post-hatch. Parents with enlarged broods produced more fledged chicks than parents with control and reduced brood size, but the body mass of chicks from enlarged broods were lower than that of chicks from control and reduced nest. Three weeks post-hatch, the body masses of females, but not males, that reared enlarged clutches were lower than among those rearing control and reduced broods. The return-rates of females rearing enlarged broods were lower than among those rearing control and reduced broods, but this trend was not statistically significant. These results differs somewhat from a previous study of the kittiwakes in the same study area which showed that the parents were not able to raise an additional chick, and, oreover, that females rearing enlarged clutches suffered a reduced survival.

The differences between these two studies will be discussed in context f adaptations to a stochastic environment.

PIGLIUCCI M.   Sun 24 Aug   S12   M. PIGLIUCCI

How do we go about studying the genetic basis of plasticity?

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The field of phenotypic plasticity has been shaping for most of the century, ever since Woeltereck misunderstood Johansson's definition of genotype and phenotype and coined the term "reaction norm". It is now a full fledged and mature area of research, but several of its most fundamental questions are still very much open to debate. One of these is: what are the genetic bases of phenotypic plasticity? Much recent (and controversial) debate has been framed i terms of the existence of "plasticity genes". *Plasticity genes undoubtedly exist*, insofar as we define them as genes coding for receptors of environmental signal These receptors, like phytochromes in plants or temperature sensors in reptiles, are the initiators of a cascade of effects which direct the organism toward one of series of alternative developmental pathways. On the other hand, there is clearly more to the genetics of plasticity than regulatory receptors, and probably only a minority of genes contributing to the genetic architecture of plastic responses ar in fact plasticity genes. How do we go about uncovering the existence of plastic genes, and how do these genes relate to the genetic variation for plasticity prese in natural populations? Current research on the model organism *Arabidopsis thaliana* (Brassicaceae) is devoted to the elucidation of the complex mapping function between genotype and phenotype, one of the most important challenge of evolutionary developmental biology. A combined use of candidate genes, QT mapping, and classical quantitative genetics is yielding a picture that can be use as a frame of reference for further studies on this fascinating field of inquiry in modern evolutionary biology.

PIJLS J.   Wed 27 Aug   P5   J. PIJLS

Interspecific host discrimination in insect parasitoids: a review

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Parasitoids may allocate eggs to hosts which have already been parasitized; either by a conspecific (superparasitism) or by another species (multiparasitism). To avoid super- and multiparasitism requires host discrimination (either intra- or interspecifically), *i.e.* the ability of a female parasitoid to recognize parasitized hosts from unparasitized ones. The vast majority of parasitoid species have been shown to be capable of intraspecific host dicrimination. Interspecific host discrimination, on the other hand, is claimed in the literature to be a rare ability.

We review the existing literature and show that this claim is not justified: interspecific host discrimination is a common and widespread ability, occurring in two thirds of the species tested and in 11 Hymenopteran families. Intraspecific host discrimination is, however, found significantly more often: in nearly ninety per cent of the species in the same data set.

The literature review was used to investigate several, not mutually exclusive, hypotheses why interspecific host discrimination has evolved less often than intraspecific host discrimination, and/or why it is more difficult to detect. The occurrence of multiparasitism is associated with a larger offspring survival probability than its avoidance. This indicates that multiparasitism can be functional. The effect was stronger among sympatric than among allopatric species combinations, supporting the hypothesis that interspecific host discrimination cannot *a priori* be expected between allopatric species. Multiparasitism is more often avoided between related species than between less related species. Thus, tests of species with a high survival probability, tests of allopatric combinations, and constraints on the evolution of host discrimination between less related species may explain why host discrimination is found less often between than within species.

Relationships in Gesneriaceae - Cyrtandroideae inferred from cpDNA, *atpB/rbcL* spacer region sequences

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A phylogenetic analysis was carried out based on the comparison of the spacer region between the *ATP-synthetase-β-subunit* (*atpB*) gene and the *ribulose-1,5-biphosphate carboxylase* large subunit (*rbcL*) gene of the chloroplast genome. The PCR-amplified *atpB/rbcL* spacer regions were sequenced in representatives of the genera *Cyrtandra, Didymocarpus, Didissandra, Monophyllaea, Rhynchoglossum*, and *Paraboea*. In the ten *Cyrtandra* species studied 83 variable positions were found over a length of 890 bp. Although the intrageneric variation was low, the resulting relationships provide insights into the colonization patterns of the South Pacific islands (Hawaii, Samoa, Fiji). With respect to generic relationships, the *atpB/rbcL* spacer region turned out as an excellent marker to investigate the phylogeny. Members of the tribes Cyrtandreae and Didymocarpeae appear closely related: the genetic divergency (2.2%) between the consensus sequence of *Cyrtandra* (Cyrtandreae) and the investigated *Didymocarpus* species (Didymocarpeae) is only slightly higher than the average distance within *Cyrtandra* (1.9%). On the other hand, members of the Epithemateae (=Klugieae) hold a clearly separated position. The promoter regions for the *atpB* and *rbcL* genes, which have been described from Rubiaceae, were identified and found to be located at homologous positions. Of the two *atpB* promoters found in Rubiaceae only the distal one appears functional, the proximal promoter has been eroded by mutations and is disrupted in *Didissandra* by a 14 bp insertion.

Life history evolution in *Sparganium erectum*: the consequences of metapopulation and local selection constraints

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The majority of water plants combine sexual reproduction with some means of clonal multiplication. Previous genetic and ecological studies revealed conspicuous differences of the sexual *vs* asexual balance among aquatic plant populations. Changes in a population successionnal status lead to major modifications in selective constraints that act on life history traits. Within this theoretical framework, we compared the importance of both clonal and sexual reproduction in young and mature populations of the European aquatic macrophyte *Sparganium erectum* (Bur-reed). The comparison of life history traits was carried out in a controlled environment experiment in order to analyse the relative importance of genetic variation and phenotypic plasticity.

We found the highest investment to sexual reproduction in the newly established populations whereas the lowest investment to sex was detected in the older populations. These life history patterns reflect the loss of sexual reproduction at the population level. We suggest that a mixed reproductive system could be maintained in the species by the interaction of two levels of selection: selection at the population level favouring genotypes with high competitive abilities, i.e. highly clonal genotypes, and selection at the metapopulation level favouring genotypes with a great dispersal potential, i.e. with a high seed production.

Phylogeny reconstruction using microsatellites

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The usefulness of microsatellite loci in phylogenetic reconstruction beyond the subpopulation level has been less successful than expected. Various factors may have contributed to this, including constraints on the range of repeat scores, asymmetry in the mutation process, and degradation of microsatellites over time, all of which may vary among loci depending on motif and location. These factors may affect both the accuracy and linearity of distance measures, thus inhibiting their performance in phylogenetic reconstruction. The importance of these various factors in microsatellite evolution is still unclear, but greater understanding is expected by making predictions based on simplified models incorporating them, and by collecting appropriate datasets capable of testing those predictions. The consequences of these factors on accuracy and phylogenetic reconstruction can also be predicted.

For example, methods of estimating range constraints and mutation rates under the assumptions of a symmetric stepwise mutation model with reflecting boundaries have been developed. The evolutionary behavior of microsatellites under this model were analyzed, and least squares procedures were employed to improve molecular distance estimation for use in phylogenetic reconstruction in the case where range constraints and mutation rates vary across loci. Range constraints are seen to have a substantial impact on phylogenetic conclusions based on molecular distances, particularly for more divergent taxa. It is also seen that in order to make accurate phylogenetic inferences under range constraints, a larger number of loci are required than in their absence. Considerations in the application of these methods to established and planned datasets are discussed.

Why do hosts accept cuckoo chicks?

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Cuckoo chicks are cared for by their hosts despite obviously differing in appearance from host chicks and despite the heavy fitness cost raising cuckoo chicks imposes on the host. In contrast hosts sometimes eject cuckoo eggs which show mimicry of host eggs. The difference between host behaviour to cuckoo chicks and eggs has been explained by i) evolutionary time-lag, ii) errors in recognising cuckoo chicks, iii) the cost of mistakes when learning is by imprinting and iv) supernormal stimuli. None of these explanations are convincing. We show that host acceptance of cuckoo chicks has evolved because of cuckoo retaliatory behaviour against hosts that eject chicks. Host ejection of cuckoo eggs persists in the face of cuckoo retaliation because it occurs early in the season and carries less serious fitness consequences for the host.

PONCET V. Tue 26 Aug S23 V. PONCET

Domestication process in pearl millet (*Pennisetum glaucum*): assessment o the genetic organisation

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Pearl millet (*Pennisetum glaucum*) and its wild relatives (*P. mollissimum* and *P. violaceum*) belong to the same primary gene pool and are still currently found i a sympatric situation in some areas in Africa. Despite the gene flow occuring between these two outcrossing forms, their phenotypic differences -the "domestication syndrome"- are maintained. It has been suggested that domestication in allogamous reproductive systems could have been facilitated by linkage of genes involved in the domestication process. The objective of this study was to map the mendelian factors controlling the domestication syndrome traits in pearl millet. An F2 population derived from a cross between a cultivated form (cv. "Souna") and a wild form (*P. mollissimum*) was analysed. Thirty five RFLP and STS markers representative of the whole genetic map were used. Twenty seven characters, describing the spikelet structure (shedding hability, seed coating...), the plant architecture (tillering habit,...) and yield parameters, were measured. Majority of the major genetic factors controlling the domestication syndrome turned out to be localised on few of the seven linkage groups of the genome. Moreover, genes and QTLs involved in the spikelet structure were located on the linkage group 6 and some of them on the linkage group 7. Another cross involving a cultivated form having a different evolutionary history has been studied to compare the localisation and the number of QTLs detected within the two crosses. Finally, comparative mapping of the domestication syndrome genes in the grass family and inferences on the dynamic of the domestication process will be discussed.

Genetic diversity in sexual and parthenogenetic freshwater planarians, *Dugesia polychroa*, revealed by allozyme electrophoresis

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In the free-living, hermaphroditic flatworm *Dugesia polychroa* (Platyhelminthes, Tricladida), diploid sexual and polyploid parthenogenetic biotypes are known. Parthenogenesis is sperm-dependent, which means that sperm is used only to initiate egg development. Sexuals and parthenogens can be found in allopatry or in sympatry. When sexuals and parthenogens coexist, bidirectional genetic exchange is possible: parthenogenetic lineages are assumed to originate from sexuals, and as parthenogens continue to produce viable sperm, parthenogens are able to fertilise eggs of sexuals. This could lead to frequent and independent origins of new parthenogenetic lineages.

We used allozyme electrophoresis to study 17 different populations from the Netherlands, southern Germany and Italy. Pure parthenogenetic populations from the Netherlands and Germany have similar multilocus genotypes. Coexisting sexuals and parthenogens from Italy share the same alleles, indicating common ancestry, recent origin of parthenogens and/or gene flow between sexuals and parthenogens. In Lago di Caldonazzo (Northern Italy), allozyme electrophoresis revealed high genotypic diversity among parthenogens, but allozyme variability within coexisting sexuals was too low for analyses of intra-population genetic structure. Presently, we are using microsatellites to analyse the small-scale geographic population structure in sexual populations of *D. polychroa*.

Evolutionary dynamics of a conserved satellite DNA present in beetles of the genus *Pimelia* (Tenebrionidae)

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Satellite DNA is a component present in all eukaryotic genomes in regions of low recombination which often differs significantly in sequence composition and abundance even among closely related species. Satellite DNA sequences of darkling beetles of the genus *Pimelia* have been characterized from 25 species/populations of which 15 are island endemics to the Canary archipelago. Southern and dot-blot experiments show a remarkable conservation of a satellite DNA family of about 355 bp in all examined species. Sequence data from about 100 clones obtained by cleaving the genomic DNA with *EcoRI, HaeIII* or *ClaI* confirms this conservation which refers both to monomeric size and sequence. This satellite is about 70 % A+T rich, with an abundance up to 45 % of the genomic DNA (roughly equivalent to 4.5 x 10^5 copies per haploid genome) and shows chromosomal pericentromeric location. UPGMA trees obtained indicate a close relationship among Iberian species, with very high intra- and interspecific sequence similarities. In contrast, in spite of a relatively recent evolutionary origin for some of the Canarian species (less than 2 My) they show higher sequence distances, in some cases with intraspecific similarities in the range of the interspecific ones. The satellite monomeric sequences show capability to induce DNA curvature. Conservation of the *Pimelia* satDNA could be related to the preservation of this curvature resulting in a higher order helical structure which may act as a specific protein binding domain.

POST R.J.   Mon 25 Aug   S20b   R.J. POST

Are populations of the *Simulium damnosum* complex on the island of Bioko isolated from mainland immigration?

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Sibling species of the *Simulium damnosum* complex (Diptera: Simuliidae) are vectors of river blindness in West Africa. A proposal to eliminate the disease from the island of Bioko depends upon the island being isolated from recolonisation by flies from the mainland. Evidence for this will be assessed by examining data from DNA, isoenzyme variation, chromosomes and morphology.

Trade-off between vegetative and sexual reproduction in the clonal plant *Ranunculus reptans*

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The creeping herb *Ranunculus reptans* can reproduce both sexually and vegetatively by the opportunity of individual nodes to produce a flower and/or one to several branches and/or roots. To investigate the genetical and physiological basis of trade-offs between clonal growth and sexual reproduction, I experimentally manipulated the allocation pattern by flower bud removal. Vegetative offspring of 12 genotypes were raised and half of the plants were experimentally prevented from flowering by cutting off the buds, while the other half was hand-pollinated. Plant size and allocation were measured as number and proportion of nodes that (attempted to) flower, rooted or branched.

The results indicate high costs of sexual reproduction because bud removal increased plant size by up to 80%. Bud removal did not affect the proportion of flowering attempts, rooting or branching nodes. Genotypes differed significantly both in overall plant size and allocation pattern, but did not interact with bud removal. A positive correlation was found between vegetative growth (no of side branches or no of rooting nodes) and sexual reproduction (no of flowers or no attempt to produce flowers). However, corrected by plant size, a genetical trade-off between the proportion of flowering and rooting nodes became apparent. This suggests that (1) bud removal influenced only overall plant size but not the allocation strategy, (2) that an existing genetic trade-off between vegetative and sexual reproduction can be masked by large size variation and (3) that plant size itself did not influence the allocation pattern. The existence of a genetic trade-off between vegetative and sexual reproduction constrains the evolution of plant life-history, since an adaptive increase in one mode of reproduction is coupled to a decrease in the other.

Cost of reproduction of female bank voles *Clethrionomys glareolus* in north Finland.

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A fundamental question in life-history theory is what determines the amount of resources an individual allocate to reproduction. In particular, the reproductive effort may depend on individual state, measured for example in terms of individual condition (like weight) or individual history (like previous reproductions). This is also related to the cost of reproduction, i.e., a decrease of survival and/or reproductive probability of an individual caused by an increase in reproductive effort.

We have studied the reproductive decision and the survival probability of females bank voles *Clethrionomys glareolus* in north Finland, Pallasjärvi. Adult females may breed many times in one breeding season.

We have used capture-recapture multi-state modelling to study 1) the monthly survival probability, 2) the probability of maturation of sub-adults, and 3) the reproductive probability of females, as a function of previous reproductive events and/or individual weight.

Microsatellite markers as a tool to investigate population genetic structure and gene flow in the endemic Mediterranean seagrass *Posidonia oceanica.*

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Microsatellite repeat sequences were applied as DNA markers to determine population genetic structure and gene flow in the endemic Mediterranean seagrass *Posidonia oceanica*, widespread in the whole basin. Marine angiosperms reproduce both sexually and clonally determining the presence of clonal patches in a population. The study of genetic diversity of these complex and highly productive ecosystems becomes important in the definition of management and conservation strategies in coastal areas.

Previous analyses on genetic diversity of *P. oceanica* detected very low levels of minisatellite polymorphism (multilocus DNA fingerprinting and RAPD-PCR) within and between populations in the Western Mediterranean basin.

In the present study, six microsatellite markers detected higher levels of polymorphism in six populations sampled along the coasts of Italy and Corsica. The number of alleles per locus ranged from 1.5 to 2.0 and the percent of polymorphic loci ranged from 50% to 83% in the different populations. Only the 33% of distinct genotypes were present in the total of 120 individuals analyzed and homozygosity resulted to be high within populations (F_{IS}= 0.206). The number of migrants per generation was variable for the different loci (Nm= 0.158-1.428), and private alleles were found in few meadows and in different stands within the same meadow. Distance analysis showed a clear genetic disjunction between the northern and the central-southern populations.

It could be established: clonal growth is important in the maintenance of *P. oceanica* populations, some of which resulted to be composed by clonal patches of different size, undergoing to limited inbreeding; gene flow exists among populations, but local forces determine genetic disjunction along a latitudinal gradient. In conclusion, microsatellites are powerful markers in detecting genetic variability in clonal species, and as such, can have a wide application in population genetic studies of marine vascular plants.

Relation between genetic structure and growth, survival and susceptibility to industrial pollution in forest tree populations

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There are indications that the effects of abiotic factors are connected with directional selection processes in forest tree populations. However, less is known about the relations between genetic parameters and genetic structure of such populations to vitality, survival and susceptibility to industrial pollution. Numerous populations were planted together in common gardens at a number of sites differing in pollution stress. Populations of Pinus sylvestris L. and Picea abies (L.) Karst. were studied to evaluate possible linkages between their genetic structure and their response to environmental stress. Significant differences were found between studied populations in number of alleles per locus, expected and observed heterozygosity and also genotype polymorphism indices. Differences in heterozygosity, genotype polymorphism indices and number of alleles per locus were related to differences among population in growth decline, radial growth and plant mortality. Also, on average the studied genetic parameters were higher for populations under stress than for their replicate populations in unpolluted control sites.

Genetic correlations and microevolutionary trajectories of migratory behaviour in the blackcap, *Syliva atricapilla*

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Migratory birds are characterised by a number of physiological, morphological and behavioural adaptations to the migratory journey. If this migratory syndrome is to persist through periods of selection for any of these traits, genetic correlations between these traits are to be expected. Here we analyse genetic correlations among incidence, amount, onset and termination of migratory activity with the aim of assessing likely trajectories of evolutionary changes in the intensity and timing of migration. We studied a total of 781 birds from a partially migratory population, and 561 birds from a completely migratory population, including not only birds from the wild but also birds from different breeding experiments, and selection lines.

The analyses of variances and covariances indicate that:

1) Incidence and amount of migratory activity are different aspects of the same trait ($r_g \sim 1$).
2) Onset and amount of migratory activity are, as expected from the phenotypic correlation between these traits on the species level, highly genetically correlated ($r_g > 0.8$).
3) Additive genetic variance in the onset of migration is low, and genetic correlations between this and the other migratory traits studied are moderate to low (and not statistically different from zero).

Our results suggest that some migratory traits are to a considerable extent genetically integrated, and therefore, evolution for some combinations of traits may be highly constrained. Considering heritabilities and genetic correlations, evolutionary trajectories for changes in migratory behaviour can be predicted; for example, we expect selection for later departure to the wintering quarters to be accompanied by shortening of the migration distance - i.e. a shift of the wintering quarters towards the breeding grounds -, and by an increase of the number of resident individuals. These results are of crucial importance for predicting evolutionary changes of migratory behaviour in consequence of global warming.

A multi-locus model of the selection barrier between populations.

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Species are reproductively separated in nature by various kinds of genetic barriers. One of the postzygotic mechanisms that may contribute to the formation of isolation barrier may be selection against the introgression of new genetic material from one to another population. To quantify the strength of arising selection barrier, Zhivotovsky and Christiansen introduced the notion of the strength of 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 under weak viability selection on multiple loci with pairwise epistatic interactions among them. We generalize this model for the arbitrary distance between populations and arbitrary epistatic interactions among loci. The strength of the selection barrier is obtained in terms of initial differences in gene frequencies and linkage disequilibria between populations. The case of stabilizing selection on additive quantitative trait is considered, in which the strength of the selection barrier is represented in terms of the variance components. We run computer simulations showing the robustness of the analytical approximations.

The evolution of recombination under multilocus selection and migration.

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We examine the evolution of recombination in a multi-locus model with viability selection and migration between two populations. In different populations weak epistatic selection favors different alleles, leading to the stable migration-selection balance under sufficiently weak migration. The conditions under which the rates of recombination will evolve due to a selectively neutral modifier locus are determined in terms of additive gene effects, pairwise epistasis, degree of linkage of the modifier locus to the selected loci and migration rates. The increased recombination is favoured if epistasis is negative (synergistic) and relatively strong. Obtained result is compared to the existing models of the evolution of recombination under mutation-selection balance, suggesting that migration can play qualitively different role in the evolution of recombination.

A recent effectives decrease of a french rabbit population, due to a viral epidemic, had no severe effects on genetic variation of microsatellite loci

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Some rabbit microsatellite loci were isolated in our laboratory (Mougel et al., Animal Genetics, in press) and nine of them are currently used to study the history of european rabbit wild populations (*Oryctolagus cuniculus*).
The polymorphism of these molecular markers allows to study the genetic structure and diversity of populations.

A correct analysis of these microsatellite data needs to take into consideration the effects of social organization, history of populations (bottlenecks, founder effects...) and mutation rates on the evolution of microsatellite polymorphism.

A french rabbit population (Versailles, France) was studied from 1982 to 1996. This population underwent a severe viral epidemy of VHD (Viral Haemolytic Disease) in 1995 leading to a 90% mortality. Allele distributions, genetic diversity and polymorphism of microsatellite loci were analysed for samples collected in 1982, 1994 (before epidemy) and 1996 (after epidemy) and compared.
The genetic diversity did not drastically fall down after the important size decrease observed in this population.

Effects of flower number on pollen transfer in three hermaphroditic species.

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The relationship between the number of open flowers and pollen transfer to stigmas was estimated in three insect-pollinated species (*Cynoglossum officinale*, *Echium vulgare* and *Oenothera erythrocepala*) in 1995 and 1996, using fluorescent dye as pollen analogue. Dye was applied to an equal number of flowers of a small, a medium and a large plant.

In *Cynoglossum officinale* and in *Echium vulgare* large plants received more visits per flower. In *Oenothera erythrocepala* no difference in number of visits per flower was found between small and large plants.

Geitonogamous pollination clearly occurred in all species. In *Cynoglossum officinale* large plants transferred more pollen per flower within the same plant (geitonogamy) and an equal or a slightly smaller amount between plants, than small plants. As a result total pollen transfer per flower increased in both years with increasing flower number. In *Echium vulgare* and in *Oenothera erythrocepala* large plants transferred more pollen per flower within the plant (pollen discounting), but a significantly lower amount per flower to other plants in the populations compared to small plants. For both these species, there is no difference in total pollen transfer between small and large plants.

In general, the male fitness curve is decelerating. We discuss this in relation to the pollen donation hypothesis.

Genetic differentiation and dispersal among *Chironomus riparius* (Diptera, Chironomidae) and *Orchesella cincta* (Collembola, Entomobryidae) populations in relation to heavy metal resistance

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Saprotrophic arthropods are exposed to a large number of potentially toxic chemicals due to pollution of their natural habitat. Among these chemicals, contamination by heavy metals is an obvious example since they accumulate in soils and sediments. Because of their toxicity and persistence, contamination by heavy metals is a good example of how natural selection acts in nature.

In this lecture two examples of this model will be given:

Allozyme frequencies of the midge *Chironomus riparius* (Diptera, Chironomidae) were assessed at four localities differing in heavy metal concentrations in the contaminated Dommel River. No correlation was found between allele frequencies and contamination. A complete absence of population substructuring was observed and gene flow among and between sampled sites was high, irrespective of the level of contamination at the particular locations. A significant deficit of heterozygote genotypes was found at all nine polymorphic allozyme-loci and at all locations sampled. Several possible explanations are discussed. Embedded in an ecological framework, allozyme analysis is considered as a useful tool to explain genetical structures within *Chironomus riparius* populations in relation to contamination by heavy-metals.

The population genetic structure among 11 populations differing in level of heavy metal contamination of the springtail *Orchesella cincta* was examined using AFLP markers. Since this study has just recently started the first preliminary results will be discussed.

Ecological complexity and the maintenance of genetic variation

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The maintenance of genetic variation is a central problem in evolutionary biology. We tested the hypothesis that environmental heterogeneity promotes the maintenance of genetic variation by allowing replicate populations of *Pseudomonas fluorescens* to evolve in structured and unstructured environments. In structured environments *P. fluorescens* populations became genetically diverse due to niche specialization and maintenance of this diversity was directly attributable to environmental heterogeneity. Populations of *P. fluorescens* evolving in unstructured environments showed no phenotypic diversification. The ecological and evolutionary dynamics associated with adaptive radiation of *P. fluorescens* in both environments were highly repeatable. Niche specialization among adaptive mutants from the structured environment was confirmed by pairwise and three-way competition experiments and also by the ability of populations consisting of single niche-specialist genotypes to produce genetically diverse populations comprised of the other niche-specialists. Competition among the three most common niche-specialists revealed that one of the three possible pairwise interactions is stable while the other two are unstable, indicating that complex ecological interactions are involved in the maintenance of genetic diversity in this system. A genetic analysis of one niche-specialist (termed WS) has revealed the phenotypic and probable genotypic targets of selection. Inactivation of genes necessary for expression of the phenotypic target of selection prevented the WS genotype from colonizing its usual niche. Selection experiments between two ancestral genotypes which differed (as a result of gene disruption) in their ability to generate by mutation the WS genotype, reveals the tight linkage between genotype and specificity of adaptation.

Conflict and reproductive manipulation in insect societies

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Insect societies are characterized by both conflict and cooperation among nestmates. Conflict and cooperation are consequences of the two non-exclusive means by which workers can enhance their inclusive fitness: 1) **working** to increase the number of reproductives (queens and males) produced by their colony; 2) **manipulating** reproduction to favor the production of reproductives of greater kin value to themselves. Manipulation is a consequence of the non-clonal kin structure of most insect societies.

In the social Hymenoptera reproductive conflict can occur around many aspects of reproduction, of which male production, queen production, and sex allocation are probably the most important, and have received the greatest attention from researchers. But conflict can also occur around other aspects of reproduction, such as caste development, colony life history, and colony division. Conflict can occur among individuals or among groups of individuals. For example, sex ratio conflict in a colony with a single queen is between the queen and the workers as a group. There is no conflict among the workers. However, conflict over male production occurs both among the workers and between workers and queen.

When conflict among individuals occurs, what is the evolutionary outcome? Which party will be able to manipulate colony reproduction to enhance its inclusive fitness? There is no single or easy answer. Each area of conflict must be considered on its own merits. Factors of importance include the kin structure of the colony, the costs and benefits of manipulation, and the "power" of each party. Details of the biology of the species can be important, such as how brood are reared. In general, only adult workers and queens are considered to have "power"—males and brood are considered to have zero power, although there are exceptional cases where this is not so. Power and control and likely to be strong where an effective and low-cost mechanism exists for manipulating reproduction. An example of this is worker policing in the honey bee. Here the interests of the queen and the workers as a group coincide to oppose male production by individual workers. Killing of worker-laid eggs, "worker policing", provides the mechanism. Queen-laid eggs are recognized by the presence of a queen-produced egg-marking pheromone.

Variation in filtering screens of *Daphnia galeata*: phenotypic adaptation to feeding conditions and genotypic differences

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Several clones of *Daphnia galeata* waterflea, a common grazer in many types of lakes, were reared with different food regimes to study their adaptation to feeding conditions. Of these animals, the life history parameters were recorded and food filtering structures were measured. At low food concentration, daphnids had larger filter screens than at high food concentration. In *Daphnia*, filter screen size is positively correlated with filtering rate. When the responses of several clones from two habitats differing in food availability (mesotrophic vs hypertrophic lake) were compared, no significant differences between the populations neither in life history parameters nor filtering structures were found. There were more differences within populations than between populations. All the clones were, however, very plastic.

By feeding the animals with food types differing in size, shape and nutritional value, information about the effects of different food sources on total area and fine structure i.e. mesh size of the filter screens were obtained. Again, the area of filter screens at high concentration of good quality food was the smallest and at low concentration the largest. On high concentration of low quality food, the size of the filter screen was intermediate. Supplementing the food with clay particles had no effect on the response of the animals. From these results it can be concluded that, besides concentration, also nutritional value of the food is an important factor affecting the phenotypic response of the filtering screens in *Daphnia*.

Pollen heteromorphism: developmental models of meiotic cytokinesis for the production of multiple phenotypes.

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Pollen grain heteromorphism is common in non-magnoliid dicotyledons: in more than 30% of the species, several types of pollen morphs, differing in their aperture number are found in all the anthers of a single individual plant. Apertures are openings in the pollen grain wall allowing regulation of pollen volume, water balance, communication between pollen grains and the stigmatic surface and germination of the pollen tubes. Therefore their number and distribution strongly influence pollen grain survival and competition capacities.

Pollen grains with four apertures germinate faster but survive less long than pollen grain with three apertures. A game theory model has shown that heteromorphism which is a mixed strategy can be an ESS when pollination condition are heterogeneous.

To complete the selective approach of pollen heteromorphism we are studying pollen grain development in order to answer the following questions:

- what are the ontogenetic constraints acting on pollen grain morphology and do the constraints restrict the number of morphs available to a single plant ?
- is it easy for a plant to produce several pollen morphs ?
- is there a cost of producing several morphs of pollen ?

Aperture number is defined early after the completion of meiosis and is linked to cytokinetic processes leading to the partitioning of the pollen mother cell into four microspores. We are using models and experiments to understand what kind of spatial relationships and what modifications of these relationships could explain aperture number definition and distribution at pollen grain surface.

The pattern of female arrival at the mating site in the yellow dung fly *Scathophaga stercoraria* represents a mixed ESS

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In most of the former work concerning the yellow dung fly *Scathophaga stercoraria* male behaviour, e.g. the copulation time, is seen to be adaptive whereas that of the females is assumed to be formed by constraints. In this study the arrival of females at the mating site, fresh cattle droppings, is investigated. Whereas almost all males are present shortly after deposition of the pat females arrive at a low, decreasing rate over an interval of about five hours. It is hypothesized that the distribution of female arrival times represents a mixed ESS formed by different trade-offs between costs and benefits of early and late arrival. Early arrival is favoured by advantages due to the decreasing opportunity for oviposition, the dung warmth reducing the time of egg development or benefits in terms of larval competition for early laid clutches; late arrival is favoured by negative effects of male-male competition on females being less strong later after deposition. To test the hypothesis computer simulations with distributions of arrival times deviating from the natural one were performed to "measure" the costs for females arriving at different times. These costs were compared with benefits corresponding to the females` arrival times calculated from assumed functions, thus giving fitness estimates. This procedure revealed that females coming to the pat delayed in a population of females arriving shortly after deposition would be favoured. In a population arriving according to a uniform distribution early females would have a fitness advantage. Thus evolution would lead to an intermediate distribution of arrival times, as it occurs in nature. Therefore it is suggested that the pattern of female arrival represents a mixed ESS as it follows the definition of this concept. This means that in *S. stercoraria* the female arrival behaviour is probably adaptive. Besides, the simulation revealed that the intensity of sexual selection by male-male competition is highest with the natural pattern of female arrival. Therefore natural selection generating this pattern as a by-product amplifies the intensity of male-male interaction.

Host-parasite interactions and the evolution of clutch size

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Ectoparasites can reduce the quality and number of offspring of their bird hosts, thereby lowering the value of a current brood. This poses the question of how ectoparasites affect trade-offs and evolution of life-history traits such as clutch size. First, evidence that the life-cycle length of the common ectoparasite species of a given host species determines whether it is more profitable for the host to raise a large or a small brood will be discussed for several host-parasite systems. Second, the evidence for behavioural host responses, favoured by natural selection and serving to reduce the parasites' impact, will be analysed. Third, the effect of host responses on the trade-off between current and future reproduction will be discussed. If parasites affect the present rather than the future brood, one possible response is an increase in current reproductive effort. Parents forced by an ectoparasite to increase their reproductive investment may have fewer resources to allocate to parasite defence, and thereby impair their own future reproduction by increasing their susceptibility to other pathogens, e.g. blood parasites. Evidence for this trade-off will be presented.

RIGAUD T. Sun 24 Aug S2 T. RIGAUD

The evolution of sex determining mechanisms in isopod crustaceans : is the heterogamety evolution driven by genomic conflicts ?

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Sex is determined by non-Mendelian genetic elements overriding the sex factors carried by the heterochromosomes in some species of terrestrial isopods. A bacterium *Wolbachia* and a non-bacterial feminizing factor (f) can both force chromosomal males of *Armadillidium vulgare* to become phenotypic functional females. The feminizing factors can be considered to be selfish genetic elements because they bias their host's sex ratio to increase their own transmission. New sex determining genes are selected (genes resisting the feminizing effects, or the transmission of feminizing elements) as a consequence of the conflict between these elements and the rest of the host's genome.

In isopods species in which genetic sex determination occur, the heterochromosomes are poorly differentiated, the two heterogametic systems (♂XY / ♀XX and ♂ZZ / ♀WZ) coexist within the same genus and even within the same species. We can therefore suppose that the evolution of sex chromosomes in isopods is at an incipient stage. Based on the observations in *A. vulgare*, and on a computer simulation, we propose that feminizing factors can lead to the evolution of heterogamety. Their presence can lead to selection of a XX/XY system from a primitive ZZ/WZ system. The consequences of this selection on heterochromosome evolution and differentiation are discussed.

Molecular evolution of microbial defense systems

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Bacteria possess a diversity of defense systems. Colicins, a heterogeneous family of toxic proteins produced by Escherichia coli, have served as a model system with which to explore the molecular mechanisms of toxin diversification and adaptation. Studies employing the combined methods of phenotypic and genotypic surveys of natural populations, experimental evolution and DNA sequence comparison suggest that two evolutionary forces likely play dominant roles in the evolution of colicins. Recombination clearly plays a dominant role in the origin of new colicin classes. Further, some form of frequency dependent selection (perhaps diversifying selection) appears to play a dominant role in additional diversification observed within existing colicin classes. The combined forces of recombination and positive selection have thus resulted in a large and diverse class of antimicrobial toxins.

Prezygotic mechanisms of incipient speciation in *Littorina saxatilis* (Gastropoda: Prosobranchia)

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Two morphs of *L. saxatilis* coexist and hybridize in sympatry i Galician exposed rocky shores. Moreover, they show incipient reproductive isolation capable of further evolving towards complete speciation. We have sampled mated and non mated individuals from the hybrid zone along an extense geographical area, and performed mate choice laboratory experiments and computer simulations to quantify the mechanisms contributing to reproductive isolation.

True copulating (male-female) pairs showed high and significant assortative mating between morphs (Yule's V=0.77) and size (Pearson r=0.59), while false copulations (male-male and male-juvenile) presented in average half of the former values. Males of both morphs mounted other snails and mated with false partners in laboratory randomly, but mated assortatively with females. Monte Carlo simulations showed that the observed non-random morph microdistribution could account for half of the morph and size correlations in true mating pairs. Behavioural mate choice mechanisms were simulated on raw data, assuming different preference/discriminant mating rules and rates, to obtain the observed morph and size relationships in pairs. None of the simulated mechanisms could explain alone both the morph and size relationships. However, a behavioural discriminant rule affecting pure morphs, plus the snail microdistribution, could explain 100% of the incipient reproductive isolation, and most of the size relationship. All results taken together do not support the reinforcement model and are discussed in relation to other alternative speciation mechanisms proposed in the literature.

ROLFF J. Wed 27 Aug '96 J. ROLFF

Better hosts dive: the life-cycle of ectoparasitic water mites and the interaction with the oviposition behaviour of their damselfly hosts

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Water mite larvae parasitizing damselflies must detach while the host is in a suitable reproduction habitat for both, parasites and itself. They should do so during host's oviposition.

Here, I present experimental data for the detachment rate of water mite larvae from two different host species, *Coenagrion hastulatum* and *Coenagrion puella*, in relation to host's oviposition behaviour. *C. hastulatum* oviposits submerged whereas *C. puella* oviposits at the water surface and aggregates with other damselflies.

It was found that mite larvae detach with a significantly higher ratio from hosts with submerged ovipositon. Experimental tests showed that this is not a species specific effect. It is mainly caused by the oviposition behaviour. The results are discussed in the light of the evolution of different mating systems in damselflies.

Evolution of reproductive effort in a metapopulation.

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Population extinction, and consequently demographic and genetic disequilibrium, could well be a common ecological event through stochastic habitat disturbance or succession. The metapopulation concept allows us to assume that the equilibrium is achieved at a higher level, while each local population is in disequilibrium. Metapopulation models allow us to understand the evolution of traits that do not experience the same selective forces in each local population. Reproductive effort could be such a trait.

The "reproductive effort model" originally suggested by Williams (1966) postulates that at any age an individual can allocate a fraction r, the reproductive effort, of its resources to reproduction and the remainder to maintenance. This partitioning of resources generates a trade off between survival probability and fecundity at every age, and selection should favor different age-specific patterns of reproductive effort during early or late stages of ecological succession. The metapopulation approach thus appears particularly relevant to study the evolution of reproductive effort in spatially structured populations experiencing succession.

We study how local extinctions and local demographic disequilibrium affect the evolution of reproductive effort in a species with overlapping generations but no senescence. We show that in a metapopulation with saturation of all sites, local extinctions simply constitute an additional source of extrinsic mortality and favor higher reproductive efforts. When the saturation hypothesis is relaxed, non trivial predictions arise. In particular we predict that larger reproductive effort may be selected for in habitats of poorer productivity, contrariwise to what would be predicted in a single population. Also, we predict that higher dispersal rates should favor selection for lower reproductive effort. However, metapopulation parameters that favor high dispersal rate also favor larger reproductive efforts.

Wing pattern plasticity in *Bicyclus*: what factor triggers seasonal forms?

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Bicyclus butterflies (Lepidoptera, Satyridae) exhibit wing pattern plasticity: butterflies which passed their final larval instars under high temperature have large eyespots whereas butterflies which developed under low temperature have small eyespots. Species living in seasonal environments exhibit seasonal polyphenism, which is reminiscent of plasticity but without a range of intermediate forms. Wing pattern plasticity/polyphenism is supposed to have an antipredator function: active butterflies during the wet season need large apparent eyespots to deflect predator attacks whereas inert butterflies during the dry season need a cryptic wing pattern. Hence, when the system works, a positive correlation is expected between temperature and rainfall. Such a correlation exists in Southern Africa, but is absent in localities situated north of the equator where *Bicyclus* species also occur. Therefore it is considered that a high temperature is a good predictor for wet seasonal forms in some parts of Africa but certainly not in other parts. Other factors like development time in connection to food plant quality will be proposed to control the induction of seasonal forms.

RUIZ LINARES A. Mon 25 Aug S18 A. RUIZ LINARES

Matriarchal phylogeny of the geese (*Anserini*)

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We have sequenced the mitochondrial control region and adjacent tRNAglu from 15 goose species/subspecies belonging to genera *Anser* and *Branta*. Furthermore, the hypervariable 5' area of the control region was sequences from additional individuals in order to get an overview of the intraspecific variation.

In a phylogenetic tree both genus *Anser* and *Branta* formed monophyletic groups with a mean divergence of 11% between the genera. The pairwise distances of *Anser* species were smaller than those of *Branta* indicating closer relationship and more recent speciation of *Anser* species compared to *Branta*.

We found a nuclear mitochondrial-like sequence that existed in all but one of the *Anser* species studied. This pseudogene could be used as an outgroup and also estimates of the relative rate of mutations in nuclear DNA versus mitochondrial control region were calculated.

Genetic polymorphism in prey choice of a soil-inhabiting predatory mite

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Arthropod predators usually feed on many different prey types. This phenomenon may arise in various ways depending on the flexibility of prey choice.At one extreme populations are an ensemble of pure specialists for each prey type and at the other they are composed of generalists that indiscriminately seize the prey encountered. In between these extremes populations may be composed of generalist predators with learned or genetically fixed prey preferences. If there is a cost to flexibility and availability of each prey is constant in time or relative to each other, selection is expected to favour genetically fixed prey preferences (specialist or generalist with fixed choice). However, the more the availability of each prey type fluctuates relative to each other, the more selective advantage is gained by generalists of the flexible kind despite the costs involved. Since generalists tend to level off relative differences in prey availability, they create selective advantages for the specialists, whereas the specialists may cause predator-prey cycles and alter relative prey availability thereby creating selective advantages to the generalist.The outcome, while still in need of a rigorous mathematical analysis, may well be that predator populations exhibits complex polymorphisms in flexible andfixed prey choices.Here, we report on experimental evidence supporting this view. A sample consisting of c. 150 individuals of the haplo-diploid predatory mite, *Hypoaspis aculeifer*, obtained from c. 0.5 m^2 sandy soil in a lily field near Breezand (North-Holland), was subject to selection in prey choice experiments with two species of astigmatic mites as prey (*Rhizoglyphus robini* and *Tyrophagus putrescentiae*, further referred to as **R** and T). Individual female predators choosing exclusively R or exclusively T in three 10-minute dual-choice tests carried out at three-day intervals were set apart and reared (on T) as isofemale lines. Selection during four generations yielded 3 lines with high probability of choosing R and 2 lines choosing T. Cross-breeding in both directions resulted in hybrid females with intermediate preferences andthe choices found in females from F2-backcrosses were best explained by simple monogenic inheritance. These data demonstrate that local predator populations exhibit genetic polymorphisms in prey preferences.

Heterozygosity and extinction in a buttefly metapopulation

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The reduction in fitness due to inbreeding, well documented in artificial settings, has led to the enduring hypothesis that inbreeding depression could be a potentially important factor determining population performance in nature. However, no field studies have been able to investigate this question critically. We have studied a large metapopulation of the Glanville fritillary butterfly (Melitaea cinxia) in SW Finland, and have found that the risk of local extinction, between autumn 1995-96, in a set of 43 small local populations was significantly negatively correlated with average heterozygosity, assayed at enzyme and microsatellite loci. Our analysis takes into account other potentially confounding variables also affecting the risk of population extinction. Low levels of heterozygosity are generated in this system by breeding among close relatives in the often very small local populations. Furthermore, there is suggestive evidence indicating that larval survival, longevity of adult females and egg hatching rate are the mechanistic causes underlying the observed relationship between heterozygosity and population extinction.

Phenotypic plasticity within individuals

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The growth and differentiation of lateral branches change when the top of a plant is removed or damaged. This is but an example of common phenomena:plasticity in response to the internal environment is expressed by parts of an organism. The variable developmental fate is evident for cells, tissues and, in plants, even entire organs. A central concept to be developed is that such plasticity could be the origin, in both mechanistic and evolutionary senses, of the more commonly studied plasticity seen in comparisons of individuals in different environments. Heteromorphisms would be extreme cases of intra-individual plasticity, representing special evolutionary adaptations.

An example to be considered in relative detail is the fate of the smaller of two branches of experimental pea plants. This branch is actively killed if it is subjected to both darkness and the inhibitory effects of another branch on the same plant, situated in a better environment. In conditions that prevent vigorous development the influence of the larger branch can suffice to kill the weaker one even when both are in the same light environment. Internal and external environments could be integrated by their modifying the outcome of a continued competition between potentially equal developmental alternatives, such as the various branches of the same plant.

Ontogeny, especially in plants, is a complex system of long-term processes. Plasticity could thus be required for adjustments to expected and chance events resulting from development itself. Further, the form of the plant and its cellular patterns could result from an 'epigenetic selection' of the best available possibilities. This would mean that the development of complex organisms has components which resemble Darwinian evolution, though they select an overall predictable result from many genetically - identical alternatives.

These traits of ontogenetic development could be the basis as well as the constraints of phenotypic plasticity.

Mitochondrial DNA analysis in Eurasian populations

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DNA sequences of the hypervariable segment I in the mitochondrial control region were analysed from 17 Eurasian populations. Eleven of the populations base their subsistence on agriculture and six of them live on non-agricultural basis. When analysing genetic distances among them, we found that whereas the agriculturalist groups are closely related to each other, the food-gatherers differ as much from each other as they do from the agriculturalist groups. Interestingly, language phyla do not seem to correlate with mitochondrial data in Eurasia, since the Uralic speaking agruculturalist groups are not to be closer related to the non-agriculturalist groups, that speak Uralic-Yukhagir languages than to other agirucultarist groups that speak e.g Indo-European languages. Thus, subsistence patterns seem to be a more decisive factor than language in shaping the diversity of the mtDNA gene pool in northern and western Eurasia.

Phylogenetic identification of a possible origin of the human T-cell lymphotropic virus type II (HTLV-II) South European epidemics among injecting drug users (IDUs).

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The complete nucleotide sequence of a human T-cell lymphotropic virus type II (HTLV-II) isolate, from the Italian injecting drug user Gu, was obtained, representing the first entire sequence of an European HTLV-II isolate. Two subgroups are described for this human retrovirus: HTLV-IIa and HTLV-IIb. The HTLV-II-Gu genome was more similar to the HTLV-IIb-NRA (98.4%) and HTLV-IIb-G12 (98.2%) strains than to HTLV-IIa-Mo (95.2%) strain. The definition of HTLV-II-Gu as IIb subtype was confirmed by restriction analysis. A phylogenetic analysis was performed by using the methods of neighbour-joining and parsimony with bootstrapping, and maximum likelihood. The different gene regions were analyzed separately, by comparing Gu with all other HTLV-II strains presently available. In the LTR, as well as in other genome regions, a clear separation between IIa and IIb was evident, and within the IIb subtype three clusters were present of which two were well supported, one containing exclusively Amerindian strains and another including all Italian and Spanish strains together with two strains obtained from New York drug users. These results suggest that HTLV-II-Gu and other IIb South European isolates were probably derived from North American IIb isolates. It is temptative to speculate that a limited number of infections from Italian/Spanish-USA/IDU connections, no more than 50 years ago, are responsible for the HTLV-II epidemic in Italy and Spain.

GENETIC STRUCTURE AND CONSERVATION BIOLOGY OF FRESHWATER CRAYFISH (*AUSTROPOTAMOBIUS PALLIPES*) IN ITALY.

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The white clawed crayfish *Austropotamobius pallipes* is distributed in the British Isles and south-western Europe (Laurent, 1988); various subspecies were recognized, among which two are found in Italy: *A. p. pallipes* in the Northwest, and *A. p. italicus* in the rest of country.

Thirty-seven natural populations of freshwater crayfish from Italy and one from France were investigated by allozyme analysis of 29 loci. Populations from France, Piedmont and Western Liguria (*A. p. pallipes*) showed alternative alleles at 6 diagnostic loci from those of eastern, central and southern Italy (*A. p. italicus*). Their average genetic distance is D_{Nei}=0.27, a value often found between distinct congeneric species of crustacean decapods (Nevo, 1984). Marked genetic heterogeneity was detected within *A. p. italicus*, whereas *A. p. pallipes* was rather homogeneous. Genetic analysis of populations from a contact area between *A. p. pallipes* and *A. p. italicus*, located in Ligurian Apennine, showed lack of gene flow, although paleointrogression events were evidenced. Accordingly, the two taxa can be considered as distinct biological species, whose reproductive isolation was presumably completed only recently in secondary contact. The levels of genetic variability found in *A. pallipes* and *A. italicus* are very low: H_e=0.015 (range 0-0.039); most populations of both species showed complete lack of polymorphic enzyme loci. Higher values of genetic variability were detected in introgressed populations from the contact zone (H_e up to 0.09). Such low genetic variability is presumably related to water pollution and habitat disturbance, which caused drastic loss of suitable habitats, leading to population fragmentation, whith marked reduction of effective size numbers; therefore, genetic drift phenomena seem to be the main cause both of genetic erosion, and of genetic heterogeneity found in *A. italicus*.

Freshwater crayfish are severely endangered of extinction (IUCN Invertebrate Red Data Book, 1983). Possible programs of reintroduction and restoration of genetic diversty of *A. pallipes* and *A. italicus* are discussed, carrierd out from populations with higher levels of heterozygosity and/or with differentiated allele frequencies.

MtDNA phylogeography of European hedgehogs

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European hedgehogs belong to the genus *Eurinaceus*, and are distributed across Europe to the Urals and from Scandinavia to Turkey. Two species are recognised, *E. europaeus* from western Europe, and *E. concolor* from eastern Europe. It has long been recognised that each of these two species is partitioned into several subspecies on the basis of morphological characters but all attempts to discretely define subspecies have failed.

In this study we constructed a mtDNA gene phylogeny to investigate genetic relationships among taxa, possible colonisation routes and the influence of range contraction/expansion on European hedgehogs.

The analysis of the spatial genetic structure of the studied populations revealed clear geographic partitioning of the haplotypes with a considerable divergence between genomes occurring in different regions of the species range. Maximum parsimony analysis and Tamura-Nei estimates of levels of genetic differentiation have shown that the two European species, *E. europaeus* and *E. concolor* are both subdivided into two major clades.

Our findings suggest a strong influence of Pleistocene isolation in southern refugia on the current genetic structure of populations.

Cytoplasmic male sterility in plants: molecular evidence and the nucleocytoplasmic conflict

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A much debated issue in plant evolutionary biology concerns the maintenance of a high frequency of male sterility in natural populations. For the past decade, a theoretical framework has been provided by the concept of nucleocytoplasmic conflict.

The genetic information contained in the eukaryotic cell can be subdivided into its nuclear and cytoplasmic components. These different genomic subsets are submitted to variable selection pressures according to their own mode of inheritance. The uniparental mode of inheritance that predominates among cytoplasmic factors, and the biparental inheritance that predominates among sexually reproducing nuclear genes generate a situation where interests are radically at variance. This creates the potential for a conflict between nuclear and cytoplasmic genes, especially with respect to sex determination.

Recent molecular studies on cytoplasmic male sterility indicates that novel chimeric genes, resulting from duplications and rearrangements of mitochondrial DNA sequences are involved in its control. Thus, male sterility, which is phenotypically the loss of the male function, is encoded by a new mitochondrial function at the molecular level. Molecular data are in agreement with theoretical models that consider cytoplasmic male sterility as a stage in the coevolution between nucleus and mitochondria, and not simply as a deleterious mitochondrial mutation.

Genetic variation in life history traits in Arabidopsis and relatives

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Arabidopsis thaliana is a predominantly selfing species. It has close outcrossing relatives such as *Arabis petraea.* The ecology and life history in the wild of the plant molecular biology model species is poorly known. Existing literature on the life history of *Arabidopsis* and relatives will be reviewed. Variation in growth and flowering traits in Danish, Swedish, Finnish and Russian populations of *A. thaliana* were studied in common garden experiments. The same populations were also studied with respect to microsatellite and enzyme marker loci. The northernmost populations had little variability in quantitative traits, consistent with lack of variation at marker loci. The southernmost populations were variable both for markers and for the quantitative traits. The populations were highly differentiated for both quantitative traits and markers (Fst = 0.6). Founder effects may result in lack of variation after colonisation events in the northern marginal populations. Similar experiments are underway with *Arabis petraea*, to obtain comparisons on level of variability in related species with different breeding systems.

The number of self-incompatibility alleles maintained in a finite, subdivided population

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In a seminal and controversial paper, Wright (1939) founded population genetics theory for single-locus, multi-allelic gametophytic self-incompatibility. Using the diffusion approximation he calculated the number of self-incompatibility alleles maintained by selection and mutation in a finite population. Though later much criticised by Moran and Fisher, the theory has been shown to give fairly accurate predictions. Wright also extended the theory to a subdivided population (the *n*-island model) and claimed that restricted migration increases the number of self-incompatibility alleles maintained for a population of a given size appreciably, because different alleles are maintained in different subpopulations.

Stochastic simulations were performed to check the accuracy of Wright's predictions. The results confirm the accuracy for a panmictic population. However, for a subdivided population, the number of self-incompatibility alleles maintained is far less than predicted by Wright. When the mutation rate is low (i.e. $< 10^{-5}$), an intermediate level of migration ($0.1<Nm<1$) even decreases the number of alleles below the value for the panmictic case. The implications of these unexpected results for the interpretation of experimental data are discussed.

Wright, S. (1939). The distribution of self-sterility alleles in populations. *Genetics*, **24**, 538-552.

Selfish, shameless, and disloyal: *Wolbachia*'s rise to success

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Wolbachia is an endosymbiotic bacterium in many arthropods, known to cause various alterations in its host's reproduction, *e.g.*, cytoplasmic incompatibility, feminisation and parthenogenesis. Although it is normally vertically transmitted (*i.e.*, from mother to offspring), horizontal (infectious) transmission does appear to happen frequently enough to distort phylogenetic congruence between the bacteria and their hosts.

In this paper, we use comparative molecular phylogenetics to get an estimate of the frequency and circumstances of horizontal transmission in a number of systems, involving parasitic and phytophagous Hymenoptera. As it turns out, patterns of horizontal transmission turn up where they were not expected, and vice versa. To a certain extent, the degree of horizontal transmission explains the widespread and abundant occurrence of *Wolbachia.*

SCHLICHTING C.D. Mon 25 Aug S11 C.D. SCHLICHTING

The role of phenotypic plasticity in life history decisions

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In the not so distant past, life history ‘strategies’ were perceived as genetically-based adaptations to local environmental pressures. There has been increasing recognition, however, that many (if not all) of the components of life histories may be substantially modified by the environment. Whether such plastic responses represent physiologically inescapable changes, or adaptive responses to variation in the environment is a current focus of research in many groups. Life history studies have always been ahead of the curve in explicitly taking ontogeny into account. Recently this recognition has been broadened to include organisms’ evaluation of *internal* environmental conditions, termed ontogenetic contingency or state-dependent responses. A separate line of inquiry has examined the role of the plasticity of maternal provisioning to offspring - e.g., a particular environmental cue might evoke a change in the allocation pattern of a maternal parent to seeds or eggs. I will discuss specific examples of the phenomena mentioned above.

I will also provide a general discussion of the obstacles to the evolution of adaptive plasticity of life histories. Beyond just the absence of genetic variability, there are a number of factors that determine whether an approriate response can evolve. Features of the environmental cues themselves, systems of reception, trade-offs and the integration of correlated characters all pose challenges to the production of an ‘optimal’ phenotype when conditions change.

A model of neutral evolution in haplo-diploid populations

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The neutral theory of molecular evolution predicts that the genetic distance between two species increases proportionally to the mutation rate μ. But this holds only for populations which are in equilibrium of mutation and drift. However, in case of speciation events the equilibrium is often drastically distorted.

We model haplo-diploid populations to study the effect of speciation events on mitochondrial and nuclear DNA using an infinite allele model with unlinked neutral loci.

Our model shows that it can take surprisingly long until equilibrium is reached again after speciation events depending on the effective population size N_e, the mutation rate μ and the initial heterozygosity. The substitution ratio between mitochondrial and nuclear loci is particularly large after recent speciation events. The consistency of the model is checked by means of a Monte Carlo-simulation. The expectation values of the model correspondent well with the means of the Monte Carlo-simulation. Furthermore the Monte Carlo-simulation shows that there can be variation of the genetic distance due to drift and mutation.

Parasites in socially structured populations

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Socially living hosts typically from persistent groups of closely related individuals at high local densities. This is especially the case in social insects, such as in ants, bees, or wasps. Because of the many barriers, parasites must find ways to get into the colony to begin with. A survey of known parasites of social insects highlights some of the strategies used. Furthermore, host behaviour, the effects of host mating strategies, or the consequences of colony size affect the environment of the parasites to which they have to adapt. In addition, transmission within and among colonies, as well as to offspring, poses special problems and is typcially different from other host-parasite systems. Experimental results will be discussed that elucidate how the demography of host colonies affects the evolution of parasite virulence.

Presentation of the software package Arlequin for the analysis of population genetics data.

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The Arlequin program aims at providing a large set of methods for the analysis of genetic data both at the intra- and at the inter-population level. At the population level, Arlequin can compute genetic diversity indices, either based on gene frequencies or on molecular information, estimate maximum-likelihood allele and haplotype frequencies for a large number of loci. It also implements non parametric tests of Hardy-Weinberg equilibrium and gametic disequilibrium, as well as several selective neutrality tests. The amount of population genetic structure can be estimated and tested up to 4 hierarchical levels using an Analysis of Molecular VAriance approach (AMOVA). Genetic distances based on Fst can also be computed among a set of populations.

Arlequin can specifically handle different types of genetic data, like DNA sequences, RFLPs, microsatellite data, or standard multi-locus data. The input files can consist either of allelic, haplotypic, or genotypic data.

Analyses can be easily chosen and different options can be selected through a graphical interface, allowing multiple explorations of the data set.

Effects of genetic drift in laboratory strains of the recently domesticated Mongolian gerbil (*Meriones unguiculatus*)

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The Mongolian gerbil (*Meriones unguiculatus*) is an abundant murid rodent in Mongolia. From a few animals captured in 1935, breeding strains have been developed, which are commonly used as laboratory animals today. Genetically, these strains are likely to have experienced a decline in genetic variation due to two main factors. 1. The initial establishment of the breeding strains should have caused a founder effect. 2. The remaining genetic variation of the founder population might have further declined due to inbreeding in captivity. The rationale of the present study was to quantify the decrease in genetic variation in the laboratory strains as compared to the wild population. A comparison of the total amount of genetic variation in relation to assumed effective population sizes (which might be derived from breeding schedules) was performed to identify the paramount determinant of the present genetic structure in the gerbils, i.e. either founder effects or random genetic drift.To address these questions, we investigated the genetic variation at polymorphic mitochondrial genes via sequence analysis of PCR-amplified DNA from both wild and laboratory animals. Applying the concept of Analysis of Molecular Variance (AMOVA), we aimed at describing the genetic effects of the ongoing domestication process of this young domestic animal.

Phylogeny, social behaviour and discordant evolution in Australian allodapine bees.

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The allodapine bees are unique among bees in progressively rearing their brood in a common, undivided chamber. This exposes them to a variety of selective factors that can strongly influence social evolution, such as the need for cooperative brood defence, the inability to restrict parental investment to descendent offspring, and opportunities for sib or cousin rearing created by generational overlap. They are also particularly suited for comparative approaches to social evolution because they display high levels of both inter and intra-clade variation in social and ecological attributes. They have commonly been regarded as a group that contains lineages that represent early transitions into sociality, but this view may no longer be tenable. The Australian allodapines display a full range in social organisation, from predominantly solitary nesting through to highly eusocial behaviour. Our study uses morphological and mtDNA sequence data to reconstruct phylogenies of Australia allodapines and investigates the phylogenetic distribution of key social attributes among the major clades, with special reference to the *Brevineura* group. The different data sets resulted in highly congruent trees and therefore, we combined our data in a single analysis which resulted in one most parsimonious tree. Based on this phylogenetic framework, we discuss lability and the likelihood of convergent evolution among various traits; and the discordant evolution among allodapine genera and its implications on social evolution.

The central limit theorem and benefits to group living for an Australian allodapine bee, *Exoneura bicolor.*

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Group living strategies have evolved many times in the Hymenoptera, but there is no consensus about the selective factors that may have lead to so many origins. Whilst some viewpoints have stressed the role of haplodiploidy and its effect on relatedness within social groups, other viewpoints have stressed the importance of benefits derived from group living. However, it has been shown that in many social bees, per capita brood production appears to decline with increasing group size. Wenzel and Pickering (1991) argued that such trends may be due to a form of bet hedging associated with variability in food intake as a function of group size. They suggest that the central limit theorem (CLT) may apply to group living species and that increased predictability of the number of brood that can be reared may provide an automatic benefit to group living. The CLT may be more applicable to social progressive provisioning groups where food for brood rearing is collected after eggs have been produced, rather than with mass provisioning species where females do not lay eggs until enough food is collected to provision for the brood cell.

Allodapine bees may be especially useful for testing whether the CLT provides benefits for group living. Allodapines rear their brood progressively in a communal chamber and food brought into the nest is consumed by larvae as a communal resource. In this study we examine two hypotheses: (i) that small colonies compared to larger colonies show more variation in brood reduction, because they are less able to predict food intake; and (ii) whether variation in the weight of brood decreases with increasing colony size, as predicted by the CLT. Our results indicate that there is greater variation in per capita productivity in small colonies than larger colonies, and that variation in food intake, measured as cumulative weight of brood, provides questionable support for the applicability of the CLT to the foraging behaviour of these bees.

Classic theories on symbiosis and evolution: Giglio-Tos and Kostitzin

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In the first half of the century symbiosis was regarded a major mode of evolutionary change primarily by Russian botanists and Italian zoologists. Among them Ermanno Giglio-Tos and Vladimir Alexandrovich Kostitzin stand out for incorporating symbiosis into quantified Darwinian theories aiming at completeness. For both, different forms of symbiosis were relatively common "final" outcomes of parasitism or predation in the evolution of close associations among different forms, resulting in many adaptations such as the eukaryotic organelles. They assumed that even minor changes in genotypic composition mainly due to the struggle for existence could easily result in discontinuous, qualitative morpho-functional changes, by operating on high multicellular forms through developmental constraints. Thus Giglio-Tos stressed how the generation time of a cellular type determines in a threshold way whether the resulting tissue has a polar rather than a bilateral, or a radial symmetry, so that even a minute change at such tresholds can result in a switch of symmetry.

The two substantially differed on the transmission of particulate inheritance in evolutionary relevant cases, being mostly Mendelian for Kostitzin while not so for Giglio-Tos. They also differed on how to achieve quantitation, Giglio-Tos relying on simple numerical or physical models whereas Kostitzin mostly treated analytically deterministic, continuous or discrete time models of population numbers, also concerning Mendelian differences. Since for parasitic and symbiotic interactions between two species such models would often result in numerically very different equilibria, Kostitin stressed that radical changes in the nature of their relationships could easily result from small, semi-isolated populations haphazardly switching to a different equilibrium.

Simple components of Giglio-Tos' theory were divulgated by Pierantoni's widely used textbooks, in the context of endocellular, bacterial symbioses indirectly "proving" the symbiotic origins of organelles. Although popularized in various ways by Kostitzin and d'Ancona due to World War II these achievements hardly spred outside Italy and France, and they were almost completely forgotten when the New Synthesis came to dominate the scene.

Genetic aspects of the colonisation pattern of *Ceratitis capitata* inferred from allozyme and RAPD variability data.

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The mediterranean fruit fly (medfly) *Ceratitis capitata*, is a fast colonising species which in the last hundred years has spread from its supposed origin in tropical Africa to a number of countries including the Mediterranean basin, parts of South and Central America and Australia.

The historical expansion of the species range is well documented and it has been suggested that medfly populations can be divided into three main categories: ancestral, ancient and new, represented by the sub-Saharan, Mediterranean and American populations, respectively.

The genetic aspects of the colonisation process was studied through the analysis of RAPD and allozyme variation. Nineteen wild medfly populations were collected from five regions in the species range: Africa, Extramediterranean islands (Canary and Madeira), Mediterranean region, New World and Australia. Both RAPD and allozyme approaches reveal that the geographical dispersal of medfly, from its ancestral source area (East Africa) is associated with a great reduction in variability. The pattern of decreasing variability occurs at two regional levels: in the African Mediterranean region and in the New World.

The consistency of results obtained from RAPD and enzyme data and their evolutionary implications are discussed.

Intraspecific mate preferences based on a single locus colour trait in a cichlid fish

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On *Neochromis* "blue scraper", a polymorphic cichlid of the endemic species flock of Lake Victoria, the impact of coloration on mate choice was investigated. In separate experiments sexually ripe females and males were offered mates of two morphs ("blue" [B] and "black and white" [BW]) in simultaneous choice situations. The treatment fishes were in transparent enclosures while the test fish moved freely between these enclosures. Mate preferences were determined by measuring frequencies of courtship and response to different potential mates, time spent near their enclosures, and time spent courting them.

Breeding experiments showed that the difference between the two morphs is determined by an X-chromosome-linked locus with simple dominance of BW. Mate preferences are either inherited partly independently of coloration or are imprinted: B males from BW parents preferred BW mates, while those from B parents preferred B mates. BW males (all from BW parents) preferred BW mate B females (all from B parents) preferred B males, and BW females (all from BW parents) chose randomly, suggesting persistance of an ancestral mate recognition scheme. BW has a very localized ocurrence within the wide geographical range of B and is therefore likely the derived form.

Colour polymorphisms are known from cichlids in several lakes. Frequencies of particular morphs vary greatly even between populations of one species. Morphs that are rare mutants in some, reached fixation in other species. Such species usually have a sister taxon that is anatomically very similar but fixed for the alternative colour morph. The simple genetics and the strong impact on mate preferences, together with the comparative evidence, support the hypothesis that colour polymorphism, in concert with mate choice, can lead to sympatric evolution of reproductive isolation in cichlid fish. The degree of isolation betwe morphs may critically depend on their relative abundances and on the visual conditions under which mate choice takes place.

ucleotide polymorphism in the *yellow* gene region of *Drosophila ubobscura*

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The *yellow* gene of *D. subobscura* maps at section 2B of the A(=X) chromosome. This chromosomal position is separated from the centromere by more than one euchromatic section and, thus, the strong reduction of the recombination rate that the *yellow* gene region exhibits in *D. melanogaster* is not expected in *D. subobscura.* Moreover, section 2B is located very near to one of the breakpoints of the A1 inversion. Therefore, the *yellow* gene can be used as a marker of chromosomal arrangement A1 that is polymorphic in *D. subobscura*. Nucleotide polymorphism in the *yellow* gene region has been analyzed in a natural population of *D. subobscura* from Riba-roja. Genomic DNA purified from single males was used to amplify by PCR a 5.5 kb fragment including the *yellow* gene. Subsequently, both strands of the resulting fragment were sequenced. Males were previously crossed to females of the *ch cu* strain in order to determine their arrangement for the A chromosome. A total of 10 Ast and 10 A1 alleles have been studied. Nucleotide polymorphism is estimated for each chromosomal arrangement separately in order to analyze their differentiation and infer which arrangement is ancestral. Additionally, the level of nucleotide variability in the *yellow* gene of *D. subobscura* is compared with that found in the *y-ac-sc* gene region of *D. melanogaster*. The strong reduction in nucleotide polymorphism detected in *D. melanogaster* is not expected in *D. subobscura* due to the differences in the recombination rate of the *yellow* gene region in both species.

The *Acph-1* gene region in species of the *obscura* group of *Drosophila*

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The gene coding for the lysosomal acid phosphatase-1 enzyme (*Acph-1*) of *Drosophila* was first cloned and sequenced in *D. melanogaster.* The gene has five small introns. Intron 1 is located in the 5' untranslated region whereas the remaining introns interrupt the coding region. The encoded protein, 438 amino acids long, presents several motifs highly conserved respect to vertebrate lysosomal (LAP) and prostatic (PAP) acid phosphatases. Moreover, the location of some introns appears to be conserved between *D. melanogaster* and human LAP and PAP genes. In this study, the sequence of the *Acph-1* gene region in *D. pseudoobscura, D. persimilis* and *D. miranda* is presented. These species are included in the *obscura* group of *Drosophila* and form the *pseudoobscura* cluster. Genomic DNA isolated from highly inbreed lines of the species was used as template to amplify by PCR the *Acph-1* gene region that subsequently was sequenced. When the obtained sequences are compared to that of *D. melanogaster*, a reduction in the number of introns is detected. For instance, intron 4 is not present in any of the three studied species. This intron is also absent in the human PAP and LAP genes. In contrast, the intron is present in other three species of the *obscura* group (*D. subobscura, D. madeirensis* and *D. guanche*) which clearly points out that intron 4 has been lost in the lineage leading to the species of the *pseudoobscura* cluster. Multiple alignment of the nucleotide sequences of the *Acph-1* gene region in the six species of the *obscura* group and *D. melanogaster* allows the study of divergence at synonymous and nonsynonymous positions among these species and inference of their evolutionary relationships. Additionally, protein alignment is used to detect which parts of the protein are conserved and which are evolving faster within the *obscura* group and between the *melanogaster* and *obscura* groups.

omeostatic mechanisms in the evolution of early development.

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We study the transition form single cells to primitive ulticellular organization by modelling some important features f this transition in conditions of environmental noise. Our odel is based on simple assumption about trade-offs between ates of reproduction and metabolism, the effects of primitive ommunication among cells through the diffusion of regulators, nd the structure of self-maintaining gene-circuits. We ighlight the role of homogenization of cell states and other orms of homeostasis in the evolution of early development.

Reproductive dominance in the social wasp, *Polistes carolina*

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Group nesting in *Polistes* wasps is an evolutionary problem, because reproduction is typically monopolised by one foundress, although all foundresses are reproductively competent. We studied reproductive dominance among foundresses in pre-emergence nests of *P. carolina* in Texas, USA. We tested hypothesis about relative roles of the order of arrival, size, and relatedness in determining reproductive dominance among foundresses. We did this by censusing and marking wasps in natural wild colonies, and combining this with assessment of relatedness and parentage in the nests using 7 trinucleotide microsatellite loci.

We genotyped 46 mothers, fathers (via sperm in mother's spermatheca), and 367 immature brood in 17 colonies of *P. carolina*. Using this data, we were able to assign all brood to their mother with high confidence. Reproduction in the nests was usually dominated by a single foundress, and the dominance increased during the study period. Relatedness among cofoundresses was high (r=0.73), and only in one nest a non-full sister foundresses was found among full sisters.

The order of arrival at the nest site rather than the size of the foundresses seemed to be more important to determine who became the dominant foundress. When the order of arrival was known, the dominant foundress was the first one to arrive in 7/9 cases. On the contrary, the dominant foundress was the largest one only in 5/14 cases.

Foundresses were observed to move commonly between nests. One group of foundresses moved permanently to join a related nest as a subordinate. Another group of foundresses visited unrelated nests, and tried to usurp them.

Genetic differentiation of North American colonizing populations of *Drosophila subobscura*

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The polymorphism for chromosomal arrangements has been studied in North American colonizing populations of *D.subobscura*. The sampled localities (Gilroy, Davis and Eureka in California; Medford, Salem and Woodburn in Oregon; Centralia, Arlington and Bellingham in Washington and Port Hardy in the northernmost part of Vancouver island in British Columbia) are spread over the whole distribution area of the species in North America.

Only some of the arrangements observed in the Palaearctic region have been found in North American populations due to the founder event. Seven localities (Gilroy, Davis, Eureka, Medford, Salem, Centralia and Bellingham) have been sampled more than once in different periods. These colonizing populations have differentiated not only in space but also in time since the colonization started, as shown by their genetic distances (Prevosti's distance). The standard errors of the genetic distances have also been calculated by a bootstrap approximation of the sampling distribution of the distance. This genetic differentiation shows a clinal pattern that parallels the pattern observed in Palaearctic populations.

SERRA L. Wed 27 Aug P10 L. SERRA

Intra and interspecific variability between *D. azteca* and *D. athabasc* revealed by randomly amplified polymorphic DNA

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D. azteca and *D. athabasca* are sibling species of the *affinis* subgroup whose distribution ranges overlap in Northern California and Southern Oregon Seven populations, five of which are located in this area, were studied. A to of 20 oligonucleotides were used in the analysis. Large random amplifie polymorphic DNA (RAPD) variation was found within species; nevertheless more than half the primers used in the study yielded greater difference between than within species. A total of 57% species-specific bands unique t *D. azteca* or *D. athtabasca* were obtained. A nested analysis of molecul variance (AMOVA) showed that the variance between populations withi species was significantly greater than zero for 55% of the oligonucleotide used, which provides evidence for an underlying geographical structure of thes populations. A dendrogram based on Nei's net divergence distance betwee populations was constructed using the neighbor-joining method; the localitie cluster in two clearly separated groups according to whether *D. azteca* or *D athabasca* is present in the sample. Specimens of *D. azteca* and *D. athabasc* from Salem (OR), where both species were collected together, presented th highest similarity encountered between species; however, this could b attributed to the small sample size since only two *D. azteca* individuals we found.

Developmental instability in *Lychnis viscaria* (L.) populations under genetic or environmental stress

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Developmental instability indicated by increased fluctuating asymmetry can be caused by either genetic or environmental stress. Because extinctions can be attributed broadly to these factors, fluctuating asymmetry may provide a sensitive tool for detecting such stresses. We studied the level of fluctuating asymmetry of flowers in a perennial outcrossing plant species, *Lychnis viscaria.* The degree of flower asymmetry was higher in small, isolated and marginal populations of the species range. These marginal populations also were the most homozygous ones. In the core area of the species range, flowers were more symmetrical. The level of asymmetry was correlated with both population size and heterozygosity. However, the partial correlation analysis revealed that when the impact of population size was controlled there was a significant negative relationship between fluctuating asymmetry and heterozygosity when controlling for heterozygosity no such relationship between population size and fluctuating asymmetry was found. This indicates that the amount of genetic variation is the more important factor affecting fluctuating asymmetry than the size of the population alone. Additionally, individuals subjected to a higher environmental stress have an increased level of asymmetry compared to control plants. Our data provide evidence supporting the view that the degree of fluctuating asymmetry could be used as a biological indicator of environmental and genetic stress.

Immunocompetence and good genes.

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Several life-history and physiological traits that are important components of the immunocompetence handicap hypothesis are radically different in vertebrates and invertebrates. Although the signal trait and the immune system may be linked via a simple trade-off, we present evidence that suggests the mechanism that underlies the trade-off and therefore the "good genes" that are potentially selected by females and drive the system, are different in vertebrates and invertebrates. We will discuss what these genes might be and why trying to pinpoint them is important for theoretical and empirical studies of parasite-mediated sexual selection.

Genetic variation in CTL epitope and flanking regions in Epstein-Barr Virus

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Epstein-Barr Virus (EBV), a double-stranded DNA herpesvirus, establishes a lifelong latent infection of B cells and is found in most of the human population. In healthy individuals, infection is controlled by cytotoxic T lymphocytes (CTLs) which recognise and kill B cells that present EBV peptides (epitopes) associated with major histocompatibility complex (MHC) class I molecules. CTL epitopes are specific for MHC alleles - which epitopes are presented depends on the host MHC allele as well as the sequence of the epitope. A study of one EBV epitope presented by the human MHC allele A11 showed that in isolates from the coastal regions of Papua New Guinea (PNG), where the frequency of A11 is high (54%), the epitope carried a mutation which abrogated MHC binding, thus suggesting that this mutation confers a selective advantage. However, isolates derived from the PNG highlands, where the frequency of A11 is low (3%), carried the identical mutation. This suggests that the mutation may have increased in frequency by random drift, and not through a selective advantage.

To examine this further, we analysed genetic variation in 9 different epitope sequences (249 bp) and their flanking regions (822 bp) from seven different EBV genes. The viral isolates were obtained from African, South-East Asian, PNG (highlands and lowlands), and Australian Caucasian individuals. Nucleotide diversity in all isolates was low at 0.84%, but the distribution of variation among populations was structured, with PNG isolates evolving independently from the rest. There was no obvious correlation between MHC diversity and EBV diversity for either the epitope or the flanking regions, and there was no evidence for enhanced nonsynonymous diversity in the epitope regions. There was also no correlation between the frequency of an MHC allele and the presence of epitope loss variants. In summary, our data suggest that the evolution of EBV is dominated by genetic drift and geographic structure, and that any selection pressure from the host immune system is towards epitope conservation, not diversification.

Salt tolerance in *Plantago coronopus*; responses to artificial selection in constant and heterogeneous environments

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Plantago coronopus is a species from salt marshes, beach plains and dune grasslands. These habitats are characterized by highly variable abiotic conditions, in particular soil salinity and soil water content. Theory predicts that in general selection in heterogeneous environments leads to generalists, while selection in constant environments leads to specialists. An artificial selection experiment was carried out to test these predictions, and to study associated changes in phenotypic reactions to salt. We used four different selective environments: two constant (salt or non-salt), and a slow and fast changing heterogeneous environment. Four-weeks old plants were selected on the basis of their number of leaves, a character expected to be related to plant performance.

In a constant environment there is no direct selection on plasticity. Yet, reactions to salt may change depending on the correlated responses in other environments.

A fast changing environment was imposed by alternating salt and non-salt conditions within generations. Inducible (and reversible) reactions, for instance in osmotic regulation, could then be advantageous. Alternatively, those plants may be selected that maximally exploit the periods in which no salt is present. A slow changing environment was created by alternating salt and non-salt environments each generation. Individual plants have to cope with either salt or non-salt conditions. There will be no direct advantage to reversible reactions.

Significant direct and correlated responses were found in all selective environments. Furthermore data on relative growth rates show differences between the selection lines in the way these responses were achieved.

SMITHSON A. Mon 25 Aug C3 A. SMITHSON

Deceptive Pollination in *Dactylorhiza sambucina*

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Many species of orchids do not offer their insect visitors any pollen or nectar rewards and specifically mimic no other organism, but are pollinated by non-model deception. Experimental work using captive bumblebees foraging on artificial flowers without rewards suggested that rare corolla morphs have a fitness advantage in non-model deceptive systems due to pollinator sampling patterns, and that phenotypic diversity in non-model deceptive orchids could be maintained by frequency-dependent selection. The fitness and genetic consequences of deception in *Dactylorhiza sambucina*, a non-model deceptive orchid with a stable polymorphism for corolla colour, will be discussed. The evolutionary consequences of deception will also be considered.

Mechanism of territory imprinting in birds

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Results of special experiments including ou on a displacement of eggs and nestlings undoubtedly attest that migratory birds do not have inherited knowledge of geographic position of their home land. To verify this hypothesis, in 1990 we performed an experiment on exchanging eggs between the pied flycatcher populations that inhabit on the Courish spit (55°05′N; 20°43′E) and Moscow region (55°43′N; 36°50′E). The distance between these populations is about 1000 km. 130 unincubated eggs collected in the nests of flycatchers in Moscow region were placed in nest boxes on the Courish spit. 90 nestlings hatched out of 130 eggs, and 79 young birds flew out from nests. During next years 5 (6.3%) birds from 79 nestlings were captured on the Courish spit and none bird was caught in the native population (in Moscow region). Our results confirm that birds are devoid of the inborn capacity to locate their native area. Earlier we revealed that local territory imprints in birds at the age of 30-50 days during postfledging period (Sokolov, 1991).

SOUTY-GROSSET C. Sun 24 Aug C4 C. SOUTY-GROSSET

Molecular genetic approach in conservation of the white-clawed crayfish *Austropotamobius pallipes pallipes.*

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The subspecies *Austropotamobius pallipes pallipes* is studied in France and Great Britain, where it is critically endangered owing to the degradation of habitat and to the introduction of exotic species responsible of crayfish plague; populations being greatly reduced, *A. p. pallipes* is now listed by the IUCN as being vulnerable and rare and action plan for its conservation is required. If a recovery program is to be initiated, it is primordial to know how much genetic variation is partitioned between remaining populations. Until now, studies have been hampered in crayfish by a lack of genetic markers: the only used method (allozymes) was not suitable for appreciating the genetic variation. We are the first to study mtDNA RFLP analyses in a crayfish and to show that mtDNA is a suitable diagnostic marker for measuring genetic diversity between *A.pallipes* populations through its European distribution (see session « geographical pattern of intraspecific variation »). However, we present here results about 13 French and 4 British populations of *A. p. pallipes* and find a high degree of similarity between geographically distant populations (haplotypes obtained with 11 endonucleases). Seeing that mtDNA provides greater resolution than allozymes, this apparent homogeneity is discussed according to two hypotheses: either *A. p. pallipes* could have reached England naturallly through post-glacial stream connection with France or human has recently introduced crayfish in England from French stock. Consequently this genetic homogeneity points up that any restocking program will be facilitated because management can be made at the European level. Nevertheless, nuclear DNA variation is to be estimated before definitive conclusions.

Does fish predation facilitates co-existence in a *Daphnia* species complex?

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Hybridization is a common phenomenon in water fleas of the *Daphnia - galeata - cucullata - hyalina* species complex. Earlier studies on the hybrid *D. cucullata* x *galeata* showed that a specific combination of life history characters (smaller than the larger parent *D. galeata*, but higher *r* than the smaller parent *D. cucullata*) can be advantageous in situations with intermediate fish predation pressure. Since it is well known that fish kairomones change life history characters as well as the behaviour of *Daphnia* we studied the effect of fish kairomones and predation on 5 taxa of this species complex.

We performed a competition experiment with 20 clones (identifiable using allozymes) changing food level, fish kairomones and fish predation during time, while recording the vertical distribution per clone during day and night and measuring size and reproductive traits.

Two hybrid taxa showed vertical migration, but only when food levels were high. During the period of fish predation relative densities of the *D. cucullata* x *galeata* hybrid increased from 10% to 70%. This hybrid taxa showed also the strongest increase in *r* as a reaction to fish kairomones. We conclude that fish predation might be an important factor for the co-occurrence of *Daphnia* parental taxa with their hybrids.

High levels of meiotic nondisjunction and nonrandom segregation in a chromosomal hybrid zone in the house mouse

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The recent literature on chromosomal hybrid zones in mouse and other mammals reveals that one or few "simple" heterozygous Robertsonian rearrangements cause a very low level of meiotic nondisjunction and have a slight effect on fertility (1).

Data are shown on metaphases II, not described previously, in male house mice (*Mus musculus domesticus*) caught in 1976 in a hybrid zone between a Robertsonian population with 9 centric fusions (CD; 2n=22) and a standard one (2n=40) near Rome (2). Aneuploidy frequency rises to remarkable values (up to about 50%) with increasing the number (from 1 to 4) of heterozygous centric fusions; segregation is nonrandom in multiple heterozygotes: metacentric chromosomes by one side and acrocentric ones by the other side tend to cosegregate.

These results could explain the narrowness of this hybrid zone and provide some support to the hypothesis of a significant role of Robertsonian rearrangements in reproductive isolation in this case.

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2) Spirito *et al.* (1980) Evolution, 34, 453-466.

The effect of social system on genetic structure in lions, *Panthera leo*.

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Presenter: M. Björklund

The social system of a species is of major importance for gene flow and has to be incorporated into any model hoping to produce accurate estimates of genetic structure. But how different social systems will affect the genetic structure is not always clear, although there are models developed that account for most variations in social system and other behaviors. When mate choice is the rule and dispersal is sex biased, as in most mammals and birds, distinct genetic patterns in the population can be expected to arise as a result. Social systems and mating patterns generally decrease the effective population size. Some causes and effects are intuitive, but many are not. Increased dispersal may, for example, sometimes cause a decrease in the effective population size. Only a few studies investigating the genetic structure of a population have fully accounted for behavioral effects on gene flow. Ignoring social systems often leads to an overestimation of the inbreeding effective size and an underestimation of the variance effective size.

By deploying microsatellites on 5 loci in lions this poster use some of these recent theories to evaluate the genetic structuring in 7 lion prides totaling about thirty lionesses. These prides are controlled by 14 males in 6 different coalitions. The study population reside in Selous Game Reserve, in southern Tanzania, and the territories are continuously distributed in a 700 km^2 area. Lionesses form prides of closely related individuals (sisters, cousins, mother-daughters etc.). New prides being bud-offs from already existing prides, always settle next to their home territory. This creates clusters of related individuals one level above the pride unit. Thus both the fact that prides are composed of related individuals and the restricted dispersal pattern of the females have to be included in any model trying to correctly estimate the F-statistics.

Homeobox containing genes in the life cycle of cnidarians

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Developmental control genes such as the homeobox containing genes of the *Hox* clusters appear to be somehow functionally conserved from *Drosophila* to vertebrates. Also in cnidarians several candidates for *Hox* genes have been identified. But even more difficult than to compare the DNA or protein sequences and to assign which cnidarian gene might correspond to which *Drosophila* or vertebrate gene it is to assign polyp and medusa stages of cnidarians to corresponding stages in bilaterians. The colonial polyp of a typical marine hydrozoan such as *Podocoryne carnea* resembles the solitary freshwater polyps *Hydra*. But for *Podocoryne* the bilayered polyp is just another larval stage from which the sexually mature medusae are budding of. During the budding process a third cell layer is formed between ectoderm and endoderm with a cavity. The striated muscle tissue of the medusa bell is derived from this mesoderm-like material.

Expression studies of *Podocoryne* candidates for *Hox* genes such as *cnox2-Pc*, which is similar to the *Deformed/Hox4* group, indicate that also in cnidarians homeobox containing genes can be used for the positioning along the anterior-posterior axis of the planula larva, the polyp and the medusa. However, *cnox1-Pc*, a gene similar to the *labial/Hox1* group, appears to be expressed exclusively in striated muscle in the medusa of *Podocoryne*.

Hox genes appear to be more diverged in sequence and function within cnidarian species than from *Drosophila* to vertebrates. This might just reflect the antiquity of cnidarians or suggest that the conservation of the *Hox* cluster became only important with the establishment of the bilaterian body plan.

Population structure, null alleles, and gene silencing in a highly selfing polyploid freshwater snail

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The patchy distribution of small freshwater habitats imposes physical discontinuity upon many populations of freshwater snails. Unless gene flow among established populations is sufficiently high, isolated populations can diverge genetically due to random genetic drift. In addition, the temporal instability of many freshwater habitats promotes episodes of local extinction, a process that may be balanced by colonization events stemming from other subpopulations within the total metapopulation.

I studied population genetic structure in the European stream limpet, *Ancylus fluviatilis*. Previous allozyme work has established the allotetraploid nature of extant Central European populations, and has uncovered very high selfing rates in these self-fertile hermaphrodite snails. Patterns of genetic differentiation among subpopulations, as reflected by estimates of F_{ST}, suggest very limited gene flow even at small spatial scales, thus supporting the potentially important role of genetic drift in population differentiation.

A unique feature of this system is the occurrence of segregating null alleles at many allozyme loci. Although documented in both neopolyploid ferns and angiosperms, null alleles have rarely been detected in polyploid animals. Due to the highly inbreeding mating system of *Ancylus fluviatilis*, individuals are homozygous at most polymorphic loci, facilitating the unambiguous scoring of null frequencies. The range of null frequencies found in this survey clearly indicates the effective neutrality of these nonfunctional variants.

The patchy distribution of suitable habitats and high proportions of self-fertilization might enhance the effects of genetic drift in driving null alleles to eventual fixation. Silencing of duplicate-gene expression appears to be an ongoing, dynamic process among local populations of *A. fluviatilis*, with upwards of 46% of duplicate loci estimated to have fixed nonfunctional alleles. Assuming effective population sizes smaller than about 10^4 and reasonable mutation rates to null alleles, the amount of gene silencing is compatible with neopolyploid origins of extant allotetraploid lineages (< 1 Myr). Gene silencing may have interesting implications for mating system evolution in self-fertile hermaphrodites, and may be instrumental in the build-up of postzygotic reproductive isolation, especially under a metapopulation structure.

Identification of very closely related hypotrichous ciliate species by Cleavase Fragment Length Polymorphism (CFLP) analysis of PCR amplified ITS2 sequences

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In ciliates, as in other groups of organisms, complexes of closely related species are frequently found whose members cannot be identified or discriminated by conventional techniques. Among one pair of hypotrichous ciliate species, *Stylonychia mytilus* and *S. lemnae*, even otherwise highly variable molecular marker systems provide insufficient resolution. Nevertheless, both species are genetically well separated species, at least in Europe, as has been shown by breeding experiments. We have sequenced the internal transcribed spacer regions (ITS1 and ITS2) of the ribosomal RNA genes of geographically widely separated populations of both species. For ITS1, not a single nucleotide difference could be found, either within or between species. Interspecific comparison of ITS2 sequences revealed nucleotide differences in three out of 203 positions. Putative secondary structure predictions based on helix stability calculations of the ITS2 variants using the computer programmes FOLD and SQUIGGLES showed slightly different patterns. The recently developed CFLPScan technique (CFLPScan kit from Boehringer) is a suitable method for visualizing small differences in folding patterns of single stranded DNA. The endonuclease cleavase cuts single stranded DNA just 5′of hairpin loops formed when a single strand folds back on itself, generating a collection of fragments (CFLP pattern) that is unique to that strand of DNA. In accordance with the hypothetical secondary structure models of the ITS regions, a CFLP analysis of PCR amplified ITS1 fragments showed a single band in both species and did not reveal any differences between them. In contrast, a CFLP analysis of ITS2 regions of both species revealed clear and reproducible interspecific differences in banding patterns. Thus, the CFLPScan technique using PCR amplified ITS2 fragments is a suitable method for the identification of single individuals of very similar hypotrichous ciliate species. Small sequence differences can be used for reliable and technically simple species identification purposes.

Coinciding and conflicting sexual strategies shape the soci organization of Thomas langurs

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The formation of primate groups was long considered in the light predation avoidance, food competition and male mate competition. The first t factors determine the grouping of females, the latter the distribution of males ov the groups of females. Other factors however, especially female choice and coercion, are also important. These sexual strategies will result in part coinciding and partly conflicting interests between individual males and female The effects of these individual sexual strategies on the social organization we studied in the Thomas langur (*Presbytis thomasi, Primates*), Sumatra, Indonesia

Thomas langurs are foli-frugivore primates. Within and between gro competition for food is not very strong, as expressed by the small effect th group size and female dominance rank have on maintenance behaviour reproductive success. Therefore, sexual strategies can interact with each oth relatively freely.

Groups typically consist of one adult male and several adult females (ran one to five). Solitary males and all-male bands are also found. This, i combination with the female-biased sex ratio in bisexual groups, indicates th male mate competition results in a monopolization of females. Thi monopolization is almost absolute, as females seldomly mate with males fro outside their social group. Groups have a limited life span, because at a certai point all females transfer to a new male. This has been related to an interactio between male coercion and female choice. Extra-group males try to co infanticide during between-group encounters. The effectiveness of this form male coercion increases with male tenure. As a reaction, females transfer, usuall without dependent offspring, in the period that these attacks become effectiv Their transfer is the expression of female choice for a male that is a better protecto against infanticide. The resulting changes in the composition of a group reflec changes in the reproductive interests of females, mediated by the effectiveness o male sexual strategies. Thus, the rather fluid social organization of Thoma langurs results from periods with coinciding male and female sexual strategie alternated with periods with conflicting sexual strategies.

Intron "sliding", intron phase and the diversity of intron positions

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For eukaryotic protein-coding genes, the total number of distinct intron positions discovered when homologous genes are aligned typically exceeds by several-fold the number that might have existed in a common ancestral gene. From this fact alone it can be inferred that the majority of extant intron locations cannot represent boundaries between primordial exon-mini-genes, but instead arose during eukaryotic evolution. However, if they arose by localized "sliding" of old introns to new positions, as has often been suggested, modern intron locations may tend to be **close to** ancient boundaries, and thus may provide useful information about ancient genes. Here we describe tests for the influence of intron sliding that have been applied to a large set of data. First, the frequency distribution of distances between intron positions was examined for a possible contribution from some process, such as sliding, that creates short inter-intron distances. No significant excess of short distances was found. Second, statistical tests for spatial clustering of introns were applied, since it has been suggested that sliding of introns from a small number of ancestral positions gives rise to clusters. No clustering was detected. Third, the phylogenetic distribution of individual intron positions was examined. Results again reveal no significant influence of a process that moves introns over short distances. Intron sliding, though it may occur rarely, has not contributed substantially to the diversity of intron positions. The great diversity of spliceosomal introns in eukaryotic protein-coding genes is largely or wholly attributable to addition of introns during eukaryotic evolution.

The interplay between herbivory, pollination and plant reproductive traits

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Because plants are integrated units, processes like herbivory and pollination are tied together through whole-plant responses to environmental factors. Here, I describe ways in which herbivores influence plant characters and pollination, and ways in which characters shaped by pollinators are related to herbivore success.

Plant reproductive success is typically measured through seed set; however, reproduction through pollen is responsible for half of the genes in plant populations. Allocation to male and female reproductive characters is influenced by foliar herbivory in an obligately outcrossing plant, *Raphanus raphanistrum*. Compensation for herbivory in female fitness through seed production may not always be matched by similar compensation in male reproduction. Shifts in allocation from male to female reproduction may be adaptive and not simply the result of developmental constraints. The implications of this result will be discussed.

In the second part of the talk, I will focus on the relationship between flower color, herbivore performance and plant fitness. Plants of *Raphanus sativus* produce white, purple and yellow flowers. These morphs have been shown to be differentially attractive to pollinators of different species. In particular, white flowered plants are often less preferred than yellow-flowered plants by pollinators. Despite these differences in attractiveness to pollinators, all forms are present in most radish populations. Here, I show that variation in flower color may be maintained by differences in herbivore performance on these color morphs. It is hoped that by considering selective pressures generated by a variety of different interacting species, we can better understand how traits and life-histories of organisms are shaped by the communities to which they belong.

Coexisting *Gammarus* types: A study on seasonal demographic fluctuations and hybridization behaviour.

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In order to understand the coexistence of two morphological similar but genetically differentiated *Gammarus fossarum* types we studied frequency distributions of juveniles, males and females (ovigorous and nonovigorous) over a time period of three years.

The two types, which could be distinguished by allozyme electrophoresis, showed significant distribution patterns both within and among types. These pattern were observed in all three years.

Additionally spatial separation in different microhabitats could be detected among types, as well as a time separation of reproductive maxima.

In so called „multiple-choice" experiments it was tested if the types that showed no hybridization under natural conditions, would be able to recognize each other as possible sexual partners under laboratory conditions. Interpopulational and intrapopulational formation of praecopulation were observed, but a high level of sexual isolation between the types could be measured with no difference so far between individuals of syntopic or allotopic populations.

Phenotypic plasticity: Defining the target of selection

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Recent studies of plants and other organisms have shown that plastic response to environment is a central aspect of phenotypic expression. As such, plasticity bears upon the fitness of individuals, and is subject to natural selection. Yet defining the target of selection for plastic traits is particularly difficult. The adaptive value of such traits will depend on the character states of functionally related traits as well as on the environmental context, which itself affects fitness as well as expression of plastic traits. This issue is examined using data from comparative studies of plasticity in a group of annual species in the genus *Polygonum.* These species are closely related and share a common life-history, but differ significantly in patterns of phenotypic response to major environmental factors including light, moisture, and macronutrients. These differences in plasticity are considered as examples of possible targets of selection in the *Polygonum* system.

luctuating paternity and sex ratio biasing in the ant *Formica truncorum*

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Recently empirical studies have shown that workers in several species f ants are able to manipulate sex allocation ratios in their favour. In particular, orkers of *Formica truncorum* and *F. exsecta* (in which colonies have a single ueen) have been shown to alter colony sex ratios in response to queen mating requency: Colonies headed by single-mated queens produce a preponderance f females and those headed by multiple-mated queens produce a reponderance of males. Such results strongly supports the view that kin selection is a major force in maintaining social structure in Hymenoptera.

These findings have resulted in further theoretical developments concerning the opposing interests of colony queens and their male mates, and, in particular, the interests of colony fathers. As a result of the haplodiploid sex determining system males never father sons, hence a male that ends up fathering offspring in a colony with a multiple-mated queen faces zero fitness if, as predicted by theory, the workers rear an all-male sexual brood. Males may, however, develop various mechanisms to mitigate such worker manipulation such that also colonies with multiply inseminated queens produce females. One way to accomplish this is by sperm clumping, where sperm from one of the two male mates is predominantly used in alternating bouts through time. As a result workers may perceive their queen as single-mated and would, in accordance with male preferences, rear predominantly females. In this paper we will present data on the mean and year-to-year variance of paternity shares and sex allocation in *F. truncorum*, an ant species with long-lived perennial colonies.

Parental workload, immunocompetence and the energetic costs of immune responses

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In life-history theory, it is generally assumed that a high level of reproductive effort leads to subsequent reproductive costs, but the proximate mechanisms underlying the trade-off between investment in current reproduction and future reproductive success remain largely unknown. Recent evidence indicate that parasite loads increase following a high level of reproductive effort, although it remains unclear whether this is a result of increased exposure to parasites, reduced immunocompetence, or both. By using an Enzyme-linked Immuno sorbent Assay (ELISA) we show that blue tits, *Parus caeruleus*, have suppressed humoral immune responses during parental care, and that this effect can be experimentally mitigated by preventing birds from participating in nestling feeding. These results give some support to the hypothesis that reduced immunocompetence could be a physiological mechanism mediating reproductive costs in animals.

In a second experiment, we estimated the energetic costs of mounting immune responses by measuring the basal metabolic rate (BMR) of immunized and non-immunized birds. Lowered immune responses during the costly activity of parental care could be a result of an adaptive resource reallocation strategy, whereby saved energy from suppressed immune respo ses covers the elevated costs of parental care. This hypothesis ("the adaptive resource allocati [illegible] model") has also been put forward as an explanation for supressed immune responses d production of costly secondary sexual characters (Wedekind & Folstad 1994, *Am. Nat.* **143**: 936-938). Our metabolic measurements did not support this model, however, since the energ costs of immune responses were very low (<< 8-13 % of BMR). We discuss some alternative planations for the observations that immune responses are often suppressed during costly acti ties such as reproduction.

SYVANEN M. Sun 24 Aug S24 M. SYVANEN

orizontal Gene Transfer and Patterns of Angiosperm Evolution. Michael yvanen, School of Medicine, University of California, Davis, California, USA syvanen@ucdavis.edu

Fritz Went, in 1972[1], pointed out the widespread occurrence of parallel evelopments outside angiosperm family relationships that are restricted to the ame geographical areas. He proposed that this phenomena, as well as the general henomena of parallel developments seen with vascular plants, is most easily xplained by widespread horizontal gene transfer among remotely related plants. is hypothesis suggests that asexual gene transfer among plants can be ufficiently frequent to influence the look and feel of the flora of an ecosystem. f this hypothesis is correct, it suggests that horizontal gene transfer among plants s much more widespread than it is among animals since parallel evolution on this cale has never been seen with animals. If these considerations are correct, the lant-animal difference should be apparent at the molecular level. In an earlier alysis[2], we showed that the molecular evolution of plant cytochrome-c was ifferent from that of animals. In the current work, I have extended this analysis o ribosomal RNA from plants and animals. In plants, ribosomal gene trees are ghly incongruent with trees based on morphological or other molecular haracters. In addition, molecular clock estimations for the angiosperms place the ivergence time for major plant families back approximately 250 MYA; the fossil ecord, on the other hand, shows that the angiosperm radiation occurred 110 YA. The discrepancy between molecular time estimates and paleontological stimates is not seen with animals. This forces the conclusion, as suggested by assilov[3], that angiosperms are polyphyletic. The only simple explanation for idespread parallelism, ambiguous higher taxonomic categories and angiosperm olyphyly is that the asexual transfer of genetic information between remotely elated plants is a major factor in shaping the macroevolutionary patterns of the giosperms.

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THE ORIGIN OF THE GENETIC CODE

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The genetic code is thought to have evolved before translation in the context o a metabolically complex RNA world in the form of unambiguous assignments of amino acids to trinucleotides. The former are assumed to have been covalently linked to oligonucleotide handles, whereby ribozymes were able to grab and use them as coenzymes. The ancestral adapter-amino acid synthetases could have been similar to present-day self-splicing tRNA introns. A "codon-anticodon" complex embedded in these synthetases could have played an important role in amino acid recognition. Extension of the genetic code proceeded through the takeover of nonsense “codons” by novel amino acids, related to already coded ones through precursor-product relationship (Wong pathway) and physicochemical similarity (Woese pathway). Experimental evidence accumulates showing the feasibility of such a scenario.

Hybridisation between sexual and asexual dandelions: generation of new clones

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The genus *Taraxacum* (dandelions) comprises both sexually and asexually reproducing species. The mode of reproduction is strongly correlated with the ploidy level. Sexuals are diploid (2x=16) and asexuals are triploid (3x=24). The latter reproduce through parthenogenetic development of unreduced egg cells (apomixis). However, asexuals still produce pollen although their male meiosis is highly disturbed. This enables hybridisation between sexuals and asexuals in populations were both species occur. The potential of hybridisation was investigated by hand-pollinating sexuals with pollen produced by asexuals. Seed-set was relatively low (about 18%) due to the poor quality of the pollen. The offspring was analysed with allozyme markers. The majority of the offspring appeared to be the result of self-fertilization, although sexuals are considered to be self-incompatible. Only 11% of the offspring were true hybrids, their ploidy level ranged from diploid to tetraploid. Triploid hybrids are of particular interest as they can be new asexual clones. They were tested for their mode of reproduction and showed a large variation in reproduction mode. Some triploid hybrids were indeed asexual, others were only partially asexual and one was found to reproduce sexually.

Evolution of virulence in two trematode parasites of a bivalve mollusc

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The first host in the trematode life cycle, a mollusc, is used by the parasite as a resource base for the asexual production of cercaria larvae. Therefore, the theory of virulence-evolution predicts that there will be an intense exploitation of molluscan hosts by trematodes, and consequently, a high parasite-induced host mortality. This has also been shown for a number of snail-trematode associations. We studied virulence (host mortality) of two castrating trematodes, *Rhipidocotyle campanula* and *R. fennica*, in their mollusc host, *Anodonta piscinalis*, which is a long-lived (up to 15 years) freshwater bivalve. Both parasites also share the same second host, the cyprinid fish *Rutilus rutilus*. The final hosts for *R. campanula* and *R. fennica* are the predatory fishes *Perca fluviatilis* and *Esox lucius*, respectively. In southern Finland, *R. fennica* is more abundant than *R. campanula*, whereas in northern habitats, the reverse is found. In the field, we found no evidence for differential mortality due to *R. fennica*. We suggest this may be due to a high residual reproductive value of the parasite because of a long host life span, low probability of competition by other parasites, and insignificant host defences, which may mean a lower optimal virulence than theory predicts. In the laboratory, when stressed by low oxygen, mortality among parasitized molluscs was higher than that of uninfected individuals, and *R. campanula* was more virulent than *R. fennica*. We suggest that the higher virulence of *R. campanula* is caused by its higher intensity of infection (quantity of sporocysts), and by more harmful timing of cercarial production (early summer) when compared to *R. fennica* (late summer when resouces are abundant). We also propose that alhough the early cercarial production may be costly in terms of life expectancy of *R. campanula*, it is necessary for transmission in northern habitats where the summer is short.

Sloths as arboreal herbivores : population strategies of *Bradypus* and *Choloepus*

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An arboreal herbivore is a species which is adapted to foraging in trees and includes predominantly herbage in its diet (Eisenberg 1978).

The selective pressures involved with arboreality and with folivory operate in opposite directions, as far as size and weight are concerned. There is an upper limit on weight that an arboreal animal can reach, and a lower limit on size linked to the efficiency of energy extraction from leaves, problems with detoxification, and problems of heat loss (McNab 1978, Eisenberg 1978). The different anatomical, morphological, and physiological adaptations required by this lifestyle have an indicence on life history traits.

Sloths are perhaps the most important vertebrate primary consumers in the canopy of moist Neotropical forest (Montgomery 1983). To maximize body size while minimizing body weight, sloths have sacrificed muscle mass, and this has enabled them to develop a large gut for storage and passage of food. Their metabolic rate is very low, digestion is slow, and body temperature varies according to ambient temperature.

Both sloth genera are K-selected, they have small (=1) litter size, extended parental care, long gestation periods, and low growth rates; they reach sexual maturity late for their body size, live a long time, and suffer low rates of adult mortality. Yet *Bradypus* are smaller than *Choloepus*, live in higher population densities, and are more specialized feeders. The rearing system in the exclusively folivorous *Bradypus* leads to genealogies with distinct food preferences. *Choloepus* have a wider dietary scope and they also feed on fruits.

Population structure and genetic diversity in two turkish *Castanea sativa* Mill. populations: comparison between isozyme and RAPD polymorphisms.

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Turkey is supposed a centre of origin of the european chestnut and a potential source for a genetic recovering of this species. Previous studies on turkish chestnut, based on isozyme analysis, showed a high genetic divergence between western and eastern populations. In the present work both isozyme an RAPD markers were used to investigate two populations of *C. sativa* from eastern and western Turkey with the aim to study and compare the genetic variation both at protein and DNA level.

Wintering buds from a total of 41 individuals were used. RAPD analysis was carried out on a total of 145 polymorphic bands in parallel with the isozym investigation based on 14 polymorphic loci. In order to assess the informative content of the two analyses, an information index was used equal to the number of bits necessary to identify the RAPD and isozyme scores.

RAPD genetic variability was estimated using: percentage of polymorphic primers (P_p), percentage of RAPD fragments (P_r) and a genetic diversity index (v_k) formally identical to the Kimura and Crow effective number of alleles, allowing a direct comparison with isozyme results. Simple matching index and UPGMA clustering algorithm were used to estimate the intrapopulation and interpopulation genetic differentiation.

Isozyme genetic variability was estimated using: mean number of alleles per locus (A), percentage of polymorphic loci (P_l), mean observed and expected heterozygosity (Ho, He) and effective number of alleles per locus (v_k). Nei genetic distance matrix was used for UPGMA cluster analysis

The results showed a marked congruence between the RAPD and isozyme analyses, confirmed a high degree of interpopulation genetic differentiation as well as a considerable genetic variability characterizing the turkish chestnut.

TERZIC T. Wed 27 Aug P8 T. TERZIC

Influence of reproductive success in *Drosophila subobscura* individuals homozygous for S or F allele of *Amy*-locus on viability of the progeny depending on substrate composition

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Considering the existence of frequency-dependent selection - "rare male effect" (RME) as a special kind of selection and its role in maintaining stable genetic polymorphism, represents an insufficiently explained phenomenon of population genetics. In the present study, a polymorphism for the *Amy*-locus in *Drosophila subobscura* was used as a model-system. Well known biochemical and physiological role of the α-amylase and precisely defined substrate for this enzyme provide the possibility to connect the influence of frequency of the genotypes for the *Amy*-locus on male mating success in *Drosophila subobscura* with some fitness components depending on some environmental factors. For that reason, the influence of mating frequency on viability depending on the mating type and substrate composition was examined. Different genotypes for the *Amy*-locus in *Drosophila subobscura* were kept under outbreeding conditions, while some environmental components (varying content of starch in the substrate) and the influence of RME on total genotype fitness through viability as a fitness component after the mating were studied. Mean viability values on starch and maltose showed a higher survival rate of heterogametic (S_fF_m; F_fS_m) comparing to that of homogametic (S_fS_m; F_fF_m) matings. A higher survival rate of heterogametic matings, for which RME was detect, could be related to a positive heterosis.

Evolution of extended parental care in marine peracarid crustaceans

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Several marine amphipods, isopods and tanaids provide care for their growing offspring after these have hatched from the female's brood pouch. In most species, juveniles grow to about half the adult size durin parental care. Two major categories of peracarids engaging in this reproductive strategy can be distinguished, epibenthic suspension-feeding species and endobenthic tube-/burrow-dwelling species. Small juveniles of a suspension-feeding species did not survive when separated from their parents, whereas larger juveniles did. All sizes of these epibenthic amphipods were susceptible to predation. Smal juveniles of two burrow-dwelling species survived well when separated from their parents and kept in predator-free environments. When exposed to predators survival of these orphanized juveniles significantly decreased. Small juveniles that were in deep burrows of their parents survived exposure to predators. Thus, in burrow-dwelling amphipods, parental care enhanced juvenile survival in predator treatments, whereas in the epibenthic species, parental care had no positive effect on juvenile survival in predator treatments. It is concluded that high predation pressure favored the evolution of extended parenta care in endobenthic peracarids. Other factors such as defence against conspecifics and improved feeding conditions favored the evolution of extended parental care in epibenthic suspension-feeding peracarids.

Multiple mating and male parentage in the bumble bee Bombus hypnorum as revealed by microsatellites

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Microsatellite analysis of 17 wild nests of the primitively eusocial bumble bee Bombus hypnorum revealed that the queen can mate with up to 3 different males. One of the males generally fathers most of the offspring and thus the effective number of matings is rarely above 2 which is the point were the average relatedness in the nest is below 0.5.

Males found in the nests were all produced by the queen suggesting that the queen polices the nest. In nests were the queen was absent the males were produced by the workers.

In several of the nests alien workers were found. These could not be the offspring of the nest queen but such individuals originating from the same nest could be the offspring of a mutual other queen. This suggests that nest overtake by queens is common in the spring when nests are still small and harbours only a few workers. The present queen is probably killed and the new queen takes over the workers.

The occurence of tuskless bulls in Asian elephants (*Elephas maximus*) under natural *vs.* artificial selection conditions

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Due to habitat destruction and direct exploitation by man, populations of Asian elephant - a formerly widespread species - are now patchily distributed and restricted in size. For centuries, human impact has been the paramount factor influencing population dynamics of this species. In the Asian elephant, most of the males bear tusks ("tuskers"), while a minority lacks this character ("maknas"). Only in Sri Lanka, 90% of the bulls are maknas. Females are generally tuskless. Under natural selection conditions, the selective advantage of tusks has not been fully elucidated. Field observations have not revealed any sexual selection towards either character state. However, artificial selection by man obviously favours maknas, since tuskers have been hunted for ivory. Additionally, tuskers have always been preferably captured, e.g. as temple elephants. In this framework, we developed a stochastic individuum-based simulation model for elephant populations to investigate the frequencies of tuskers and maknas under various mortality schedules for a period of 2000 years, which is the assumed time of artificial selection by man in Asian elephant populations. For the purpose of the simulation, the tusk character was assumed to be controlled by a single autosomal gene or by a major gene in a polygene system, with either dominant or recessive inheritance. Simulations were performed for several populations of Sri Lanka and Southern India, where reasonable historical data on hunting effort and population size were available. A validation by real census data supports a dominant inheritance mode of the tusk character and a slight selective advantage for tuskers under natural selection conditions. Since the model simulates both population dynamics and tusk allele frequencies under various mortality schedules, it can predict the effect of conservation efforts on populations of the Asian elephant.

TILL-BOTTRAUD I. Tue 26 Aug S1 I. TILL-BOTTRAUD

eteromorphism of cyanogenesis in white clover: one way of reducing the osts of plant defence against herbivory.

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Cyanogenesis (the release of hydrogen cyanide by bruised leaves) is a common defence mechanism in plants. In some species, such as white clover and birdsfoot trefoil, most populations show a polymorphism for both the substrate (a cyanoglucoside) and the enzyme of the reaction that leads to HCN release. The maintenance of this polymorphism was long thought to be due to two opposing forces, herbivory (favouring HCN-producing cyanogenic individuals) and frost (favouring acyanogenic individuals that cannot produce HCN). However, recent studies have shown that frost is not a direct selective factor.

In white clover a single individual produces simultaneously cyanogenic and acyanogenic leaves, cyanogenesis is thus a heteromorphic character. It is therefore difficult to infer the true genotype of a plant in natural populations and the phenotypic polymorphism may not be genetic. We suggest that cyanogenesis is a costly defence mechanism and that heteromorphism has evolved as a means to reduce this cost. We developed a game theory model showing that a mixed strategy (i.e., producing both cyanogenic and acyanogenic leaves) can be an ESS. The observed polymorphism and the distribution of the proportion of cyanogenic plants along an altitudinal gradient can be explained by a balance between herbivory pressure along the gradient and the cost of defence.

Tephritid fruit flies contain full-length *mariner* elements

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Full length *mariner* elements were isolated from three closely related species of tephritid flies:*Ceratitis capitata*, *C. rosa* and *Trirhithrum coffeae*. (Gomulski *et al.*, 1997; Torti *et al.*, submitted). Very high similarities, ranging from 90.1% to 96.4%, were found in inter and intraspecific comparisons of the elements. All the sequences contain features typical of *mariner* elements including a putative TATA box, a polyadenylation signal and the D,D34D catalytic domain motif proposed by Doak *et al.* (1994) and Robertson (1995). The majority are almost certainly non-functional as their coding regions contained deletions and frame-shifts. However, one clone *Ccmar1.18*, from *C. capitata*, was found to possess an uninterrupted ORF coding for 338 amino acids with ~ 60% similarity to the *mos*1 element of *D. mauritiana*.

Database searches and phylogenetic analyses showed that the *mariner* elements isolated in the present study are representatives of Robertson's mellifera *mariner* subfamily but they do not appear to be closely related to *mariner* elements from other tephritids previously identified by Robertson Roberston, 1993). The *mariner* elements here described form a tight cluster, ne the periphery of the mellifera subfamily. The ancestor of these elements was almost certanly present in the lineage prior to the divergence of the three species.Analysis of these elements revealed that their presence in all three species is probably due to vertical transmission rather than to other mechanism such as orizontal transmission.

The copy numbers of the elements within each species are very differen about 10 in *T. coffeae*, 500 in *C. capitata* and 5000 in *C. rosa*. These differenc in copy number could be dueto the existance of some form of self regulation, such as overproduction inhibition (OPI), or merely the result of stochastic loss, by random genetic drift.

Genetic variations in aging cohorts

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Known genetic risk-factors for major causes of death such as the D allele at the *ACE* locus in Humans are candidate genes when addressing the problem of genetic components of longevity. An association study (Schächter *et al.*, 1994) revealed potential pleiotropic age-dependent effects on longevity at this locus as the D allele was more frequent in a sample of centenarians than in adult controls.

In an effort to predict the genetic composition of a population in different age-classes for such genes, we investigate a simple model of a heterogeneous cohort composed of individuals that belong to defined groups, e.g. relevant genotypes, differing in their age-specific susceptibility to death. The immediate result derived from the model is that genotypic frequencies are expected to exhibit much more extreme variations at advanced ages than at younger ages as a result of the increase of selection among elderly people. Conditions for multimodal distributions with age are showed.

Under the assumption that mortality rates conform to the widely applicable Gompertz-Makeham equation, parameter space is explored and compared to existing values for different populations. Finally, the model is applied to the different data obtained at the *ACE* locus.

Schächter, F. *et al.* Genetic associations with human longevity at the *APOE* and *ACE* loci. *Nature Genetics* **6**, 29-32 (1994).

The specificity of adaptation in *Escherichia coli.*

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The physiological manifestation of adaptive evolutionary change was investigated in 12 replicate populations of *Escherichia coli* that were propagated for 2000 generations in a glucose-limited environment. Representative genotypes from each population were assayed for fitness relative to their common ancestor in the experimental glucose environment and in 11 novel single-nutrient environments. After 2000 generations, the 12 derived genotypes had diverged into at least six distinct phenotypic classes. The nutrients were classified into four groups based upon their uptake physiology. All 12 derived genotypes improved in fitness by similar amounts in the glucose environment, and this pattern of parallel fitness gains was also seen in those novel environments where the limiting nutrient shared uptake mechanisms with glucose. Fitness showed little or no consistent improvement, but much greater genetic variation, in novel environments where the limiting nutrient differed from glucose in its uptake mechanisms. This pattern of fitness variation in the novel nutrient environments suggests that the independently derived genotypes adapted to the glucose environment by similar, but not identical, changes in the physiological mechanisms for moving glucose across both the inner and outer membranes.

Signal divergence and reproductive isolation in a grasshopper

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The mating behaviour, including acoustic and chemical signals and mating preferences of the grasshopper *Chorthippus parallelus* (Orthoptera: Acrididae) has been studied both in a hybrid zone between parapatric species and more broadly around Europe. Originally focused on the possibility of reinforcement of prezygotic isolation in the hybrid zone, this project has now moved on to consider the causes of divergence in populations outside the zone.

We now have detailed information about the present distribution and pattern of colonisation of *parallelus* throughout Europe. Each population represents a different evolutionary history; some have been isolated for thousands of years, others have resulted from rapid post-glacial range expansion and others are sympatric with a closely related species. Utilising this variation, we can compare observed patterns of divergence with the predictions of the various theories for the origins reproductive isolation.

TRIEST L. Wed 27 Aug P2 L. TRIEST

Are hybrids and introgressed hybrids dominating in mixed populations of Primula vulgaris x Primula elatior ?

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We studied individuals belonging to several populations o morphologically pure P. vulgaris, pure P. elatior and a mixed population o presumed hybrids with clearly intermediate morphological characteristics of bo species. The goal was to assess their genetic identity and to estimate the extent o hybridization and introgression. In addition to previous research on isozymes we decided to visualize this genetic identity at DNA level through RAP analysis. Eleven decanucleotides from a set of hundred allowed an unambiguou interpretation of the obtained amplification products at species level. Princip component analysis revealed three major groupings of individuals: one group o pure Primula elatior and P. elatior-related hybrids, a second group of Primul vulgaris en P. vulgaris-related hybrids and a clearly distinct group o intermediate hybrids.

This study allowed to distinguish by DNA polymorphism analysis th pure Primula species, as well as their hybrids that seem to consist of at leas three distinguishable types. True hybridization resulting in identical F1 individuals could be clearly demonstrated. There is also evidence o introgression towards both species, whereas isozymes only indicate unidirectional introgression from P. elatior towards P. vulgaris. In a patch of 8 individuals, 44% were pure P. vulgaris, 29% were morphological hybrids wit a P. elatior genotype, 18% were true F1 hybrids and only 9% were hybrids with a P. vulgaris genotype. Hybrids and introgressed hybrids are thus locally dominating in the mixed populations.

These hybridization processes are occurring at extremely small geographical levels and show a structuring in terms of only several meters distances. The choice of amplification products that are diagnostic at species level will allow to study further the spatial structure of mixed Primula populations and to estimate the effect of habitat fragmentation on the genetic structuring of these populations.

TRIEST L. Wed 27 Aug P2 L. TRIEST

ybridization is not a dominating process in the Salix alba - Salix ragilis complex (willows)

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The polyploid Salix alba - Salix fragilis hybrid complex in Belgium is tudied using morphological characters, allozymes and DNA. Most of the orphological features show a redundancy and have a low diagnostic value for dentifying the hybrids and possible introgression patterns.

Molecular data from allozymes and Random Amplified Polymorphic NA's (RAPD) previously have been investigated on intra- and interspecific ontrolled crosses (parental types and F1) in order to make correct assumptions n the nature of the pure species and their hybrids.

A thorough screening with 15 decamer primers for PCR based olymorphism revealed 95 amplification products at species level. On the basis of genetic distances, clustering and ordination analysis, a reference system for identification of individuals has been established. The proposed reference system was then checked against additional European samples of putative pure species to ensure its reliability and is currently applied to elucidate the possible patterns of hybridization on a regional scale as well as on a local scale. In Salix alba, the allozyme data indicate a large allelic eveness, but with an overall heterozygote deficiency. Regions with an increased or even total allelic fixation of enzyme loci are present for Salix fragilis.

About 69% of the willows have a morphology corresponding to the genotype differentiation, whereas 22% of the morphological S. fragilis contained DNA fragments typical for S. alba. Dito for 8% of the morphological S. alba. The RAPD analysis, together with the allozyme divergence suggests that hybridization is not a dominating proces on the field and that both willow species have kept their gene pools well separated.

Retroviral Evolution and Distribution in the Vertebrates.

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Mammalian and avian retroviruses are well described, and they have been classified into seven genera on the basis of their phylogenetic and biochemical properties. We have been using PCR to isolate and characterise endogenous retroviruses from several other vertebrate classes, chiefly reptiles, amphibians and fish. To date we have obtained over 100 retroviral sequences and phylogenetic analysis shows that many of them are only distantly related to previously described viruses. Furthermore, these viruses often cluster within well supported clades which may represent novel retroviral genera.

However, we have found that two of the mammalian retroviral genera, the spumaviruses and murine leukaemia viruses, do appear to have counterparts with a widespread distribution within other vertebrate classes. The exogenous human and primate spumaviruses probably evolved from a group of endogenous and exogenous elements which have a distribution ranging from sharks to mammals. The murine leukaemia-related viruses, which have a host range similar to the spuma-like viruses, have a complex evolutionary history and appear to display a significant degree of co–evolution with their vertebrate host classes. Despite this, sequence analysis clearly shows that there have been two recent horizontal transfer events between distantly related hosts, one from a monotreme to a bird, and one from a placental mammal to a marsupial.

TRONTELJ P. Wed 27 Aug P11 P. TRONTELJ

enetic divergence and the species boundary in the snail leech (*Glossiphonia complanata*) species aggregate

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The snail leech inhabits freshwater habitats throughout the northern hemisphere. Many morphological types occur and some of them have been described as separate species. Their species status, however, is still under debate. In a recent study using RAPDs we could show that the European morphs *G. nebulosa* and *G. concolor* are biological species (Verovnik, Trontelj and Sket, in prep.).

We studied the genetic divergence between morphs (or supposed species) as well as between some of their spatially isolated populations by sequencing a portion of the 12S mt rDNA and the nuclear ribosomal transcribed spacers (ITS1 and ITS2). Specimens were taken from different locations in Europe and from one location in Canada. The closely related species *Hemiclepsis marginata* (from Europe) and *Placobdella ornata* (from Canada) were used as outgroups. Within each morph, all data sets show a low variability (max. 1.5 % sequence divergence) across Europe. Divergence between populations roughly reflects their geographic distance. The divergence between different European morphs is approximately 5 %. The divergence of the Canadian *G. complanata* specimen lies either within this range (12S rDNA and ITS1) or slightly exceeds it (ITS2; app. 7 %). The divergence of both outgroup species is significantly higher. In a neighbor-joining tree the Canadian specimen represents a sister group of the European cluster.

These data indicate, in addition to some previous morphological studies, that *G. complanata* (sensu lato) cannot be regarded as a single species. According to the molecular distance data, the speciation events in Europe probably took place after the Canadian population(s) was (were) separated from the European ones. The morphological heterogeneity of snail leeches makes it likely that many more separate species will be described in the future.

Evidence of Hybrid Dysgenesis in a Platyhelminth Parasite

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Processes of speciation are attributed to the evolution of genetic barriers to gene flow (i.e. isolating mechanisms) between populations (Mayr, 1963). Reproductive isolation mechanisms are numerous and vary from group to group. In previous work (Trouvé *et al.*, 1996), we have demonstrated a mate preference (assortative mating) between individuals of the same population (i.e. coming from the same geographic area) of the *Echinostoma caproni* species, an hermaphroditic parasite. This result suggests that there is a partial pre-zygotic isolation between individuals of allopatric populations and raises the question of whether such a prezygotic isolation is linked with a post-zygotic isolation process. To test this hypothesis, we quantified and compared the fecundity, a significant component of the fitness, for 2 parental populations and for their first, second and third hybrid generations. During 6 days, the number of eggs released by each worm and by day were counted. The number of eggs released per day per worm remained constant during the 3 generations in parental populations. F1 hybrids appeared as fecund as parental populations; however, the fecundity of hybrids decreased significantly on the 2nd generation and this low level of egg production remained constant in the third hybrid generation. The high decrease of fecundity, which occurs following the first genetic recombinations (i.e. in F2) could reflect a genomic incompatibility between these populations and would explain the partial pre-zygotic isolation observed.

Ref: Mayr. 1963. Harvard Univ Press. Trouvé et al. 1996. *Heredity* 77: 1-8.

he significance of attributes of sexual dimorphism for reproductive isolation etween species of the group "Myctophum asperum" (Myctophidae, Pisces)

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The disputes between of scientist about criteria species go now. Main in opinion majority are the ability to cross and to give fertile progeny. The reproductive isolation is important for formation of species in processes of evolution. Lanternfishes are one of the most of mass representatives fishes of opened ocean. For the specific identification serve various luminescent organs. Basically these are difficult organized photophores, which are located by definite series. Inside of specific group "Myctophum asperum" is totaled three species (two from them are described in comparison recently by Becker and Borodulina in 1978 and us in 1993) and at least of two forms with not clear systematic status. All fishes from this group have ctenoid scale which is attached to leather firmly and are close in colour. At all morph this group the arrangement of series photophores absolute identical, their numbers can differ only in series AO-photophores only statistic. However all maturity forms and species of this group have the external attributes sexual differentiation. These are caudal glands. At males are present supra-, and at females - infracaudal glands. The number and form these glands are simultaneously and characteristic by specific attributes of species inside of groups. At M.lunatum the specific attribute is the availability over eyes lunate glands appearing only at adult individuals. Thus, without complexities to determine the species inside of this groups it is possible only on maturity of part of population this specific of group. At series species of genera Diaphus also can not be observed specific differences in arrangements photophores. And form orbital glands can be simultaneously and sexual and specific attributes. The occurrence of specific differences on attributes being simultaneously by attributes of sexual dimorphism obvious one of directions evolution of species and process of speciation.

Plant-herbivore interactions: antagonism versus mutualism?

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Herbivores interact with their hosts at different levels of plant architecture which is created by modular growth, i.e. by repetition, differentiation, and integration of modules. These interactions can alter both plant architecture as well as life-time reproductive success, and usually the effects are detrimental for the attacked plants. Unpalatability implies less damage and, hence, unpalatable plants can spread in a population where the risk of attack is high enough. Although herbivory improves the relative fitness of unpalatable plants as compared to palatable plants, the absolute fitnesses of both plant-types decrease with the risk of herbivore encounters. This form of interaction would be the result of an antagonistic coevolution.

In some cases, shoot damage increases branching as suppressed meristems are released from apical dominance. As a result plants may partially compensate, and even to overcompensate (i.e. damaged plants produce more biomass, fruits and seeds than undamaged plants), for damage. The benefit of overcompensation is expressed as increased seed yield when the plants are attacked and damaged by herbivores, while this strategy may well incur costs on plant growth and reproduction in the absence of herbivores. This scenario differs from the antagonistic view of plant-herbivore interactions in that the absolute fitness of overcompensating plants is supposed to increase with the risk of herbivore encounters. This situation resembles the mutualistic plant-pollinator systems. However, it may be premature to let it represent mutualistic coevolution.

TURNER P. E. Thu 28 Aug S14 P. E. TURNER

Sex and the evolution of intrahost competition in RNA viruses

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Fisher and Muller argued that sex is advantageous because it allows beneficial mutations that occur in separate lineages to be fixed in the same gene pool. Without sex these favorable mutations could at best compete with each other and could not be incorporated into the same genome. For this reason, the Fisher-Muller Model predicts a faster rate of adaptation to the environment in large sexual populations in comparison to their asexual counterparts. Sexual reproduction occurs in populations of the RNA virus φ6 when multiple bacteriophages co-infect the same host cell. In this study, we sought to test the predictions of the Fisher-Muller Model by determining whether sex favors more rapid adaptation of φ6 to its bacterial host, *Pseudomonas phaseolicola*. To that end, we let populations of φ6 evolve in replicate environments that allowed either a high multiplicity-of-infection (MOI) or a low MOI (i.e., in the presence or absence of sex, respectively). In addition, these two environments should differ in the level of intrahost competition experienced by viruses, because intense within-host competition is expected only at high MOI. After 200 generations of viral evolution, all experimental populations showed a significant increase in fitness relative to a common competitor of the ancestral genotype, but we found no evidence that sex increased the rate of adaptation to the environment. Thus, our findings do not support the predictions of the Fisher-Muller Model. However, closer inspection of one viral population evolved at high MOI revealed evidence of an evolutionary tradeoff. That is, viruses evolved under conditions of high MOI are selectively favored *only* when the level of intrahost competition is intense. This may be explained by evolutionary changes in viral life-history traits such as a reduction in burst size, and/or a decrease in lag-time prior to exponential growth. Furthermore, our experimental results may be used to examine the separate effects of hard and soft selection on the evolution of RNA viruses.

TVERAA T.   Wed 27 Aug P8   T. TVERAA

Regulation of foraging trips and the costs of incubation shifts in the Antarctic petrel Thalassoica antarctica: an experiment

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In species where incubation are shared by both parents, the mate's ability to fast on the nest may constrain the time available for foraging. The decision to return to the nest should therefore be a compromise between its own foraging success and the mate's ability to fast on the nest. In order to examine how the body conditions of incubating Antarctic petrels *Thalassoica antarctica* influences both the length of foraging trips and incubation shifts, we experimentally handicapped females by increasing their flight costs during a foraging trip by adding lead weights to their legs. Handicapped females spent more time at sea and had lower body conditions at arrival to the colony than controls, and, moreover, females in poor body condition at arrival to the colony spent generally more time at sea than those with higher body condition. The prolonged time period spent at sea by handicapped females was associated with higher desertion rates than among controls. The time the incubating mates fasted increased with their body condition at arrival to the colony, suggesting that a high body condition of the incubating bird may reduce the probability of nest desertion. Accordingly, our results suggest that the time spent foraging is adjusted to the body conditions of both the foraging and the incubating mate.

Butterflies of the deep sea: on the development, possible function and evolution of eyespots in ophidiiform fishes of the genus *Neobythites*

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Several butterfly and fish species show eyspots or ocelli which resemble large vertebrate eyes. Empirical evidence suggests that these conspicuous structures serve to deter visually hunting predators or to deflect their attacks to less vital parts of the body. In fishes, eyespots have been found not only in species from shallow waters, but also in deep-sea dwellers. The ophidiiform genus *Neobythites*, for instance, occurs in tropical and subtropical oceans at depths of ca. 25 to 1800 m. A considerable number of the about 45 species belonging to this genus show one or several ocelli or eyspots at the dorsal fin. A closer examination of the ocellus in *N. stefanovi* from the deep Red Sea and the Gulf of Aden (NW Indian Ocean) revealed a geographical variation in the size and the position of the spot. The larger spot of the deeper living Red Sea population may intensify the signalling effect at greater depths. In this population eight developmental stages of the ocellus could be distinguished. While the juveniles with a still weakly developed ocellus occurred exclusively at depths of 700 - 800 m, the larger specimens with advanced ocellus developmental stages were encountered only at lesser depths. These findings indicate an upwards directed ontogenetic migration which coincides with ocellus development. The ocellus should allow adult *N. stefanovi* to gain access to more abundant food resources in shallower waters at a lower risk from visually hunting predators.

Among the different species of the genus *Neobythites* there are considerable variations in the shape, position, and number of eyspots. We discuss the possible evolutionary origin of this structures as well as questions related to their possible functions as devices for predator avoidance, species recognition, or intraspecific communication.

Bidirectional incompatibility between two cryptic species of Trichopria

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Populations of the cosmopolitan parasitoid *Trichopria Drosophilae* , a diapriid pupal parasitoid of *Drosophila*, were collected in Panama, Florida, California, several countries in East and West Africa and in Europe. Taxonomists could not detect any morphological differences between them and concluded that all populations belonged to *T.drosophilae*. However, crossings between different populations revealed that two groups exist. Within groups, interbreeding occurs, but populations belonging to different groups do not produce female offspring. Using 16S rDNA sequences and sequences of the protein coding ftsZ gene,the presence of different strains of *Wolbachia* in the *Trichopria* populations could be demonstrated. African populations and those from Panama and Florida harbour an Atc strain, while European and Californian populations harbour an Adm strain of *Wolbachia.*

Treatment with Tetracycline during 7 generations resulted in bacterium free strains from Benin and The Netherlands.Crossings between *Wolbachia* free Benin females and Dutch males resulted in female offspring and demonstrated that the bidirectional incompatibility had partially disappeared. The reciprocal cross did not result in female offspring.

Studies of the mating behaviour showed that although males always court the females of the other group, females are reluctant to mate with males from the other group.

Hybrid females do not produce offspring, when unmated, or when mated to Dutch or Beninois males.

The two groups of T.*Drosophilae* populations must thérefore be considered as two different sibling species. The role of *Wolbachia* induced bidirectional incompatibility in speciation is discussed.

The units of selection in 'viscous' host-parasite systems

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Analysis of host-microparasite models suggests that evolution of virulence in parasites should maximize the infectivity over mortality ratio (to 'maximize their R_0'). This, however, only holds in 'well-mixed' systems.; if the rate of mixing is low, local relatedness builds up, both among the parasites and the hosts. This implies that in such 'viscous' systems, there is scope for kin selection. Using a correlation dynamics approach, I analyse the characteristics of the 'unit of selection' (clusters of related individuals) of parasites and hosts. This can be used to show how less virulent parasites may replace virulent parasites virtue of their more efficient way of exploiting host clusters. For example, parasites that reduce their infectivity in order to allow their host to reproduce may invade a population of parasites that sterilize their hosts. On the other trophic level, hosts that commit suicide upon infection may invade a population of hosts that do not. Since the units of selections of both hosts and parasites includes traits of the complementary level, their 'extended phenotypes' are overlapping: hosts *and* parasites benefit when a cluster of infected hosts grows.

Muller's Ratchet, meiosis and generation of genetic variation in sexual an asexual Taraxacum

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The genus Taraxacum (dandelion) contains sexual and asexual plant lineages, may co-occur. Asexual plant lineages presumably branch from sexual ones. Asexuality in Taraxacum is associated with an increase in ploidy level, impaire male meiosis manifested as aneuploid infertile pollen, unreduced megaspores a first meiotic division restitution and subsequent parthenogenetic embryo development, and autonomous endosperm development.

It has been hypothesized that some asexual lineages may be old. In absence of meiotic recombination, slightly deleterious mutations could accumulate, with eventually a negative effect on fitness. This accumulation with negative effect fitness of asexual reproducing populations is known as Muller's Ratchet.

In this project, several characteristics are studied in a range of sexual and asex plants, using a cytogenetic and molecular based approach. Course of meiosis is followed in pollen mother cells, mostly focusing on chromosome numbers, pairing and segregation. Localization of some rDNA regions is compared by fluorescent in situ hybridization (FISH) on mitotic and meiotic chromosomes. Sequences of some "housekeeping" and meiosis related, protein coding genes be obtained. Comparison of nondegenerate and nonsynonymous substitutions, codon usage, DNA composition and rate of base substitutions should reveal the "clicking"of Muller's Ratchet in established asexual lineages. A combination o FISH and Southern blotting on pulsed-field gel filters may reveal chromosomal rearrangements that may be one way to counterbalance the negative effect of Muller's Ratchet.

VAN DE ZANDE L. Mon 25 Aug S21 L. VAN DE ZANDE

Effective population size of two bottlenecked Seychelles Warbler populations estimated from multilocus DNA fingerprint and demographic data.

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Between 1959 and 1968 the entire world population of the Seychelles Warbler (*Acrocephalus sechellensis*) consisted of 26-29 birds confined to Cousin Island. Protective measures led to a recovery of the warbler population, numbers rising to nearly 320 in 1982 which is the carrying capacity of the island. In 1988 a translocation of 29 warblers to the island of Aride was carried out. This population has grown to a present size of over 300 individuals. These features present a unique opportunity to study the effects of a bottleneck in a population that has been monitored from the time of the bottleneck onward. Multilocus DNA fingerprint analysis revealed a mean bandsharing similarity of 50% for both populations. This value is high compared to that obtained for outbred avian species, which typically average 25%. The between population similarity for Cousin and Aride is 0.97, suggesting that the translocation did not increase the level of homozygosity nor did it cause a pronounced founder effect. From the bandsharing similarity, estimates of homozygosity and hence of genetic effective population size (N_e) can be derived. For the present Cousin population this yields an estimated value of N_e of 62.5. If for the initial undisturbed Seychelles Warbler population on Cousin a bandsharing value of 0.25 is assumed, an N_e of 187.5 is obtained. Thus, it can be concluded that a substantial level of inbreeding has occurred with a decrease of N_e of 67%., even though the population has rapidly recovered. Demographic parameters yield an N_e of 59.4, slightly lower than the values derived from fingerprint data. This may be due to the fact that the mutation rate of the minisatellite loci is an uncertain factor. Alternatively, the discrepancy in the estimates of N_e might be explained by the fact that during and shortly after the bottleneck phase the demographic parameters are different from those of a population at carrying capacity.

AFLP-fingerprints identify clones in asexual dandelions (Taraxacum, Asteraceae).

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The genus Taraxacum is a textbook example of asexual reproduction by seeds in plants. Most specimens are polyploid and propagate via agamospermy, i.e. the formation of seed from parthenogenetically developing unreduced eggs. There are thousands of morphologically distinct asexually reproducing clones which are considered independent evolutionary units. A number of these are classified as 'microspecies' within 'sections' which presumably comprise all clones with common ancestral genomes.

AFLP (amplified fragment length polymorphism) was used to characterise the genetic diversity in two Danish, putatively apomictic populations. DNA was isolated from eighty field-collected plants per population Up to sixty polymorphic genetic markers per AFLP-PCR per plant were generated. Per population c. thirty genotypes were found, some appear to be common (c. ten representatives per sample), while the majority is unique, private or nearly so. Four genotypes were detected in both populations and may represent relatively wide-spread types. Individual genotypes were grouped in a phenetic tree by calculating their genetic similarity followed by UPGMA-cluster analysis. Tree structure revealed that besides truly identical genotypes, nearly identical and more distant genotypes could be distinguished. The meaning of the phenetic tree structure will be discussed, mainly with respect to clonal identification of dandelions.

VAN DER VELDE M. Wed 27 Aug P9 M. VAN DER VELDE

Microsatellite variation in the haploid moss-species *Polytrichum rmosum*

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Mosses often show low levels of morphological variation. Therefore, this kind of variation is not useful to study genetic variation between populations let alone to study genetic structure within populations. Although allozymes have proven to be very useful to discriminate between closely related *Polytrichum* species, the level of variation is very low within species (*P. formosum*: P=13.3%, H_e=.04) and does not reveal genetic differentiation een geographically distant populations.

As microsatellites generally are expected to show much higher levels of variation, we developed microsatellite primersets to study the genetic structure both between and within populations of the species *P. formosum*. Out of 26 loci, that were scorable, 14 were found to be polymorphic. Several characteristics of these microsatellite loci, like polymorphism related to average microsatellite length, number of alleles related to average 'crosatellite length and the assumed step-wise mutation process, will be discussed. Based on data from a subset of the populations previously examined for allozymes, the levels of variation observed for these microsatellites were higher than for allozymes (P=53.9%, H_e=.255). This level of genetic variation gives a resolving power that is high enough to discriminate between individuals within a population of this highly clonal species. On the other hand, we still did not observe substantial genetic differentiation between populations.

Intra- and interspecific virus transfer in *Aspergillus* species.

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In natural black *Aspergillus* populations 10% of the strains are infected with dsRNA mycoviruses. Mitochondrial classifications of infected strains show that infections are common throughout the range of different black *Aspergillus* species. These mycoviruses have a (slightly) negative effect on their hosts' fitness. Transfer of mycoviruses through the black *Aspergillus* population is inhibited by the omnipresent heterokaryon incompatibility between strains.

At the population level, deleterious elements without means of horizontal transfer should decline and disappear. So why are these black *Aspergillus* viruses so widespread in the population at such a stable frequency? Intra- and interspecific protoplast fusion experiments with black *Aspergillus* and *Aspergillus nidulans* strains show that virus transfer between heterokaryon incompatible black *Aspergillus* strains is more limited than transfer between interspecific combinations. This suggests that infection may occur interspecifically. The heterokaryon incompatibility barrier within the black *Aspergillus* species is a stronger one than the species barrier between black *Aspergilli* and *Aspergillus nidulans*!

enetic Founder Events in the Tree Species of the Krakatau Islands, ndonesia

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he vegetation of the Krakatau islands was completely destroyed during the nfamous 1883 eruptions; thus creating a rare opportunity to study a bottleneck f known severity and date. This project aims to use molecular markers to xamine the effects that bottlenecks, population size and isolation have on enetic diversity at the population level. Large collections of leaf material for NA analysis have been made. This material was preserved using the Rogstad 1992) saturated NaCl/CTAB preservation method which has made sampling in emote areas efficient and possible. The project is in the initial stages of evelopment and is currently undertaking a AFLP survey of genetic diversity n the Krakatau islands and comparative sites on the coasts Java and Sumatra.

ogstad, SH 1992 *Saturated NaCl-CTAB solution as a means of field reservation of leaves for DNA analysis*. Taxon 41:701-708.

VAN DIJK P. Sun 24 Aug S2 P. VAN DIJK

What makes a dandelion an apomict?

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Apomict plants produce seeds asexually, thus without fertilization. Abou 0.1 per cent of the angiosperms are apomicts. Often apomictic taxa ar closely related to sexually reproducing taxa. An important question for th understanding of the evolution of apomixis is that of the genetic basis o apomixis. There are many different developmental processes leading t apomictic seed production in higher plants. However, there is a strong association between apomixis and polyploidy. With the exception of a fe disputed cases of diploid apomicts, all apomicts are polyploid. This association is one-way; the great majority of polyploids are normal sexuals. We study the genetic basis of apomixis in dandelions (*Taraxacum officinale*). In this species, diploids (2x = 16) are outcrossing sexuals, whereas triploids (3x = 24) are autonomous, obligate apomicts. However, triploids also produce pollen and can be used as pollen donors in crosses. Because pollen meiosis in 3x plants is highly disturbed, offspring numbers in controlled 2x X 3x crosses are too small for segregation analysis. Therefore we have made bulk 2x X 3x crosses by placing individual 2x plants in pure 3x populations. The apomictic phenotype of the offspring was described and correlated with the DNA content as measured with a flow cytometer. A significant proportion of the plants were partial apomicts. In addition, apomictic 4x plants obtained in such crosses were used in 2x X 4x crosses, which generated a uniform 3x progeny. In this progeny segregation for apomictic reproduction was scored. The results are discussed, also in relation to some models on the genetics of apomixis in higher plants.

Evolution of amino acid biosynthetic pathways in *Buchnera aphidicola*, endosymbiont of aphids

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Nearly all aphids maintain an obligate, endosymbiotic association with *Buchnera aphidicola*, a member of the Proteobacteriaceae that is closely related to *Escherichia coli*. The bacteria are housed in specialized cells of organ-like structures (mycetomes) in the hemocoel of the aphid and are maternally transmitted. Phylogenetic studies have indicated that the association had a single origin, dated about 200-250 million years ago, and that host and endosymbiont lineages have diverged strictly in parallel.

Aphids, like other animals, are unable to synthesize 10 amino acids, which they consequently require from an external source. Their diet (phloem sap), however, is deficient in these essential nutrients and *Buchnera* has been suggested to be involved in their biosynthesis and provisioning. Physiological and metabolic studies have recently substantiated such a nutritional role. In addition, genetic studies of *Buchnera* from several aphids have revealed modifications in the biosynthetic pathways leading to the essential amino acids tryptophan and leucine. In both cases, genes encoding rate limiting enzymes were found to be transferred to plasmids. These gene amplifications have been interpreted as adaptations of *Buchnera* to the endosymbiosis, endowing it with the capacity to overproduce the essential amino acids, and hence, to contribute to the ability of aphids to thrive on a nutritionally unbalanced diet.

We have surveyed the genetic organization of the leu and trp biosynthetic pathways in *Buchnera* from several major lineages of aphids and our results indicate that: 1) *leuABCD*- and *trpEG*-encoding plasmids are more widespread than previously anticipated; 2) the transfer of these genes to different ancestral replicons has occurred multiple times during the coevolution of aphids and *Buchnera*, and; 3) certain chromosomal rearrangements of the leucine operon probably predate its transfer to plasmids, and are hypothesized to represent the first genetic modifications that allowed for moderately elevated production of leucine. We suggest that besides aphid growth kinetics as a likely component of selective pressure for gene rearrangements in *Buchnera*, the possible role of the host plant deserves attention.

Molecular characterization of the leucine gene cluster and flanking regions from the endosymbiont *Buchnera aphidicola* of the aphid *Tetraneura caerulescens* (Pemphigidae)

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Several lines of evidence suggest that nutritional interactions have been of paramount importance to the evolution of the endosymbiotic association between aphids and bacteria of the genus *Buchnera* (Proteobacteriaceae). Aphids feed on phloem sap, a diet of unbalanced composition that is particularly poor in essential amino acids. Nutritional and physiological studies have implicated *Buchnera* in the biosynthesis and provisioning of several of these essential amino acids, which aphids, like other animals, require from an external source. Recently, these findings have been paralleled by the discovery of genetic modifications in the biosynthetic pathways leading to the essential amino acids tryptophan and leucine in *Buchnera* from various aphids of the family Aphididae. These involved independent transfers to plasmids of genes encoding rate limiting enzymes, and presumably allowed for elevated production of the respective amino acids, which are thought to be made available to the aphid host.

For a better understanding of the evolution of the nutritional interactions relating to the essential amino acid leucine, knowledge of the diversity in the genetic organization of its biosynthetic pathway in *Buchnera* is a prerequisite. We have undertaken a comprehensive survey of the organization of the leucine gene cluster among major evolutionary lineages of *Buchnera*. Here, we report on the cloning and sequence analysis of a putative chromosomal DNA fragment from *Buchnera* of the aphid *Tetraneura caerulescens* that contains the *leuABCD* genes and flanking regions. The organization of the gene cluster is compared to those observed in other *Buchnera* as well as in *Buchnera*'s closest known relative, *Escherichia coli*, and a possible evolutionary scenario for the biosynthetic pathway in the endosymbiosis is discussed.

VAN HOEK A. Mon 25 Aug S9 A. VAN HOEK

volutionary aspects of the symbiosis between anaerobic ciliates and ethanogenic bacteria in the cockroach hindgut.

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Anaerobic ciliates, identified as *Nyctotherus* sp., occur in the hindgut of many cockroach species. These intestinal ciliates host endosymbiotic methanogenic bacteria. Behavioural and morphological studies suggested that the ciliates as well as their endosymbionts are different in various strains of cockroaches.

In order to study the evolutionary aspects of this symbiosis the rDNA genes of individual ciliates and their methanogenic endosymbionts were analyzed. Sequence and restriction analysis of PCR-amplified rDNA genes showed that the ciliates isolated from the various cockroach hosts differ substantially. The endosymbiotic methanogens of these ciliates, too, proved to be different. Since, in contrast to the eubacterial endosymbionts in aphids, the phylogeny of the endosymbiotic methanogens, the ciliates and their cockroach hosts does not match, we have to conclude that the symbioses between methanogenic archaea, anaerobic ciliates, and cockroaches evolved more than once.

ITS and 5SrRNA variation of different *Wolbachia* strains involved in sex-ratio distortion in arthropods

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Bacteria in the genus *Wolbachia* are widespread in arthropods and induce sex-ratio distortion or cytoplasmic incompatibility in their host. The 16S sequence data from this group suggest they are very closely related (< 3% difference) and could be subdivided into two distinct groups (type I and II). Other genes analyzed from *Wolbachia* are the bacterial cell-cycle ftsz gene (< 12% divergence) and the dnaA (< 12% divergence) gene. As these genes code for proteins, the mutation rate is expected to be lower than for non-coding regions. One such non-coding DNA region of *Wolbachia* is the intergenic spacer, which is also relatively easy to amplify as primers can be designed that bind to conserved regions of rDNA genes. A region containing a small 3'part of 23S (61bp), the intergenic spacer (66bp) (ITS) and a major part (92 bp) of the 5S gene was sequenced of different *Wolbachia* strains to determine the variation. ITS is 66 bp long for type I and 65 bp for type II *Wolbachia*. ITS variation was maximally 13.6% which is greater than 16S but similar to ftsz sequence data. The maximum variation found in 23S was 6.5% and 7.6% for 5S which is also considerably higher than in 16S. A discrepancy in variation was found between ftsz, ITS and 5S data as sometimes a high diversion rate was found for one of them but not for the other two.

Speciation Patterns and Ancestral Distributions in Albinaria inferred from ITS Sequences

Coline van Moorsel

The genus Albinaria (terrestrial snails from Greece) consists of more than 200 species and subspecies. Some of these species have a large area of distribution ranging from the Greek mainland to the Turkish coast, while others cover only very small areas. To understand the evolutionary pattern of speciation and distribution, variation between ITS sequences (ITS1 and ITS2) of the rDNA of over 60 specimens was studied. The ITS sequences revealed both highly variable and relatively conserved parts, with sequence divergence increasing from the intra-individual to the generic level. The phylogram inferred from the ITS sequences did not produce monophyletic grouping of all populations of one species. It appeared that some of these populations gave rise to new 'species'. When geographical distributions of the populations were mapped on the tree a logical pattern was obtained, with related populations having adjoining areas of distributions. Inferring the order of speciation from the tree, ancestral patterns of distribution were reconstructed.

On the consequences for conservation: stochasticity and genetics in metapopulations, a pedigree approach

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Only a few studies have analysed the effects of both genetic and stochastic processes on the risk of extinction or the vulnerability of populations. Typically, studies concentrate either on genetic effects (inbreeding depression, loss of genetic variation, accumulation of deleterious alleles) or stochastic effects (environmental, catastrophic, demograpic).
In the present study we try to explore the combined effects of inbreeding and demographic stochasticity on the viability of metapopulations of the butterfly Bicyclus anynana. Pedigrees were determined for six metapopulations and one large panmictic population over a period of eight generations. Each metapopulation consisted of four subpopulations which varied in effective population size (Ne) and amount of gene flow. Fitness traits were measured to quantify the effects of inbreeding depression. Computer simulations were run to explore the stochastic effects of biasses in sex ratio's, variance in progeny number and differences in mating succes.

Morphological variation and fitness components in relation to population size in *Silene nutans* L., a rare plant species at its western border.

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Silene nutans (Caryophyllaceae) is a rare plant species at the western margin of its continental distribution range, being comprised of small to relatively large and scattered populations. It mainly occurs on dry grasslands which were formerly extended in Western Europe and are currently restricted to small and fragmented areas as a result of habitat destruction and forest recolonization due to the abandon of traditional agro-pastoral activities. A previous study on allozymic variation showed that no genetic erosion was found in relation to population size, the small populations showing unexpectedly high levels of genetic variation.

The aims of this study are to examine offspring fitness and morphological variation in relation to population size to test the existence of inbreeding depression in populations of small size. Seeds (from two to five fruits) were collected from eight randomly chosen plants (= families) in six silicicolous populations of *Silene nutans* ranging in size from 14 to 2000 individuals. After germination in petri dishes, up to 40 seedlings per family were planted in 0.6 l pots and grown for five months in a greenhouse. During the experiment the following characters were measured: number of leaves and rosettes after 4, 10 and 22 weeks, length and width of the longest leaf of the third pair after 4 weeks, length and width of the longest leaf of the sixth pair and fresh and dry weights after 22 weeks. The results will be discussed in relation to population size, but will also be related to reproductive characteristics.

Adaptive significance of Arrhenius activation energies estimated from temperature responses of ectotherm life-histories: the case of Collembola

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Responses to temperature in ectothermic organisms are not only characterized by the lowest and the highest temperatures tolerated, but also by the plasticity of the response, defined as the rate at which development and growth increase with temperature in the intermediate range. To some extent temperature plasticity is a necessary physiological consequence of ectothermy, however, significant differences between species suggest that it may be considered as a life-history trait subject to evolution. The shape of the temperature response in the intermediate range determines the physiological time scale of the species.

To adequately describe the temperature responses of a variety of species and processes, the model formulated by Sharpe and DeMichele was used, of which the Arrhenius model is a special case. One of the parameters in this model, usually called activation energy, may be considered as a measure of temperature plasticity, and it may be estimated from experimental data using curve fitting techniques. This was applied to literature data for egg development, moulting, maturation, reproduction, ageing and metabolism of soil and litter dwelling Collembola (Hexapoda, Apterygota). A total of 141 responses, of 54 species, were analysed using various statistical methods.

Estimated Arrhenius activation energies (H_A) varied between 15 kJ/mol and 180 kJ/mol, a range in accordance with literature data on other species. Estimates for H_A did not significantly differ between the various processes in a species (development, growth, aging, etc.). This seems to indicate that temperature affects all life processes of Collembola in a similar way and that there is a single physiological time scale for each species.

When H_A was analysed for effects of ecotype (i.e. the position taken in the depth gradient of the soil), taxonomic position, or body size, ecotype appeared the best predictor of H_A. Surface-active species tend to have higher activation energies than soil-living species, while litter dwellers encompass a wide intermediate range. The fact that ecotype is a better predictor of H_A than taxonomic position demonstrates that temperature responses have evolved independent of phylogeny. The adaptive significance of high plasticity may be associated with increased seasonality among surface active species, compared to the more season-indifferent life-history of soil species.

enetic and environmental effects on character correlations under selection: hat theory predicts and what Plantago does.

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Several authors have argued that observed correlations among different characters appear to facilitate concerted responses to selection, labelling them synergistic, reinforcing, or protagonistic. In *Plantago lanceolata,* plants with long leaves also form large spikes with heavy seeds, traits that are beneficial under shady conditions. Furthermore, artificial selection on leaf length under simulated shade not only increased survival and reproduction in the shade, it also reduced germination under conditions not suitable for growth and establishment.

Such favourable correlations can not readily be explained by individual selection. A correlation is a characteristic of a population rather than an individual. Directional selection will deplete favourable (co-)variation, and antagonistic pleiotropy will retard further evolution. Thus, one would expect unfavourable rather than favourable correlations.

Therefore, we need to think about scenarios that can explain the evolution and maintenance of favourable correlation structures, 'architecture' according to some. The following possibilities are discussed:

1. Populations with favourable correlations can track temporal changes in the environment.
2. Specific adaptive landscapes give rise to favourable trait associations, as a result of the balance between selection/mutation/drift.
3. Correlations are side effects of underlying developmental processes, sometimes advantageous, sometimes not.
4. Correlation structures are the indirect results of selection for phenotypic plasticity.

VANDAMME A.M. Sun 24 Aug S20 A.M. VANDAMME

"The three human T-cell lymphotropic virus type I subtypes arose fro three geographically distinct simian reservoirs"

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To investigate the origin of human T-cell lymphotropic virus type I (HTLV-I) strains of diverse geographical origin were analysed. We sequenced the L and env genes of HTLV-I strains from Brazil, Central African Republic Taiwan and Zaire, and the simian T-cell lymphotropic virus type I (STLV-I strain PHSu1 from a baboon from the Sukhumi primate centre. We performe phylogenetic analysis using neighbour-joining, parsimony and maxim likelihood methods. Three separate HTLV-I clusters were identifie interspersed between STLV-I clusters. The Brazilian and Taiwanese strains were within the first well-supported cluster containing all cosmopolitan HTLV-I strains flanked by west African STLV-I strains. The HTLV-I strains from Central African Republic and Zaire fell into a central African cluster close to the chimpanzee STLV-I isolates. The third well-supported cluster included all Melanesian HTLV-I strains and had Indonesian STLV-I strains as closest neighbours. Therefore, currently known HTLV-I strains represent three HTLV-I subtypes that most probably have orginated from three geographically distinct interspecies transmission events. The highly divergent PHSu1, isolated from Papio hamadryas, was closely related to PCY-991, isolated from Papio cynocephalus, both from the Sukhumi primate centre. Both clustered together with Asian wild-caught rhesus macaque STLV-I strains suggesting recent interspecies transmission of virus from rhesus macaques to colony bred African baboons at the Sukhumi primate centre. In the rooted env trees obtained using the STLV strain PH969 as an outgroup, the Asian strains branched off before the African strain, implying an Asian origin for the HTLV/STLV type I based on presently available strains and methods.

he effective size of metapopulations

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e derive the long-term effective size, N_e, for a general model of population ubdivision, allowing for differential deme fitness, variable emigration and mmigration rates, extinction, colonization, and correlations across generations in ese processes. We show that various long-term measures of N_e are equivalent. e effective size of a metapopulation can be expressed in a variety of ways. At demographic equilibrium, N_e can be derived from the demography by ombining information about the ultimate contribution of each deme to the future enetic make-up of the population and Wright's F_{st}'s. The effective size is given y $N_e = 1/(1+\mathrm{var}(J)) <1-F_{st,i}>/N_i\ n$, where n is the number of demes, J_i is the ventual contribution of individuals in deme i to the whole population (scaled uch that the sum of $J_i = n$), and <> denotes an average weighted by ${}_i^2$. This formula is applied to a catastrophic extinction model (where sites are ither empty or at carrying capacity). Contrary to the expectation from the tandard island model, the usual effect of population subdivision is to *decrease* e effective size relative to a panmictic population living on the same resource.

Selection on the slope of reaction norms for butterfly wing patterns

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Many tropical nymphalid butterfly species show seasonal polyphenism associated with wet/dry seasonality. The ventral side of the wings of the wet season form (wsf) has conspicuous eyespots, whereas in the dry season form (dsf) these eyespots are almost absent. It has been suggested that the eyespots of the wsf act as deflection devices, while the dsf relies on crypsis. These forms reflect the different challenges of the two seasons: reproduction in the wet season (when food plants for the caterpillars are widely available) and survival in the dry season (when the vegetation has died off). In the light of this hypothesis one might ask to what extent the amount of plasticity in wing patterns can be changed by selection.

To answer this question we selected on the slope of reaction norms for wing patterns in the African satyrine butterfly *Bicyclus anynana*. Temperature is the main factor controlling the alternative forms in this species. We selected for high plasticity (HP) by selecting at 23.5°C extreme wsf parents. Their offspring was reared at 18.5°C and from this generation extreme dsf individuals were chosen as parents for the next (23.5°C) generation. Selection for low plasticity (LP) was done by selecting at 23.5°C for extreme dsf individuals and at 18.5°C for extreme wsf individuals. After around 12 cycles (= 24 generations) of selection we performed a split-family experiment to determine reaction norms. Full sibs of two HP lines, two LP lines and the stock were reared at 18.5, 20.5, 21.5 and 23.5°C. In addition to six wing characters, two life history traits (development time and pupal weight) were measured. The results suggest that it has not been possible to substantially increase or decrease plasticity of wing patterns. It will be argued that genetic correlations are a likely cause of this lack of response.

WINDIG J.J. Sun 24 Aug S12 J.J. WINDIG

Genetic background of phenotypic plasticity in the European Map butterfly (*Arascnia levana*)

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One of the more spectacular forms of plasticity is the wing pattern in the map butterfly *Araschnia levana*. Butterflies of the spring form have orange wings with black spots and emerge from overwintering pupae induced by short days in the larval stage. Butterflies of the summer form are black with a white band and emerge from directely developing pupae induced by long days. Offspring of wild females was split in the laboratory over short day (12h Light) and long day (16h) climate rooms. Short day larvae all produced spring forms, most long day larvae produced summer forms. Heritabilities of wing pattern characters within forms were high (>0.4) especially in the long day environment (>0.7). Genetic correlations across environments were strong (>0.7). The adult wing pattern was related to the larval development time. A simple model may explain this relation and gives rise to speculations about genes for plasticity. Another interesting aspect is that the wing pattern of each form resembles that of other butterfly species. This is discussed in the light of West-Eberhard's theory of polyphenism as a first step towards speciation.

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The major transitions as a deterministically unfolding process

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During evolution on Earth there has been a directional change where self-replicating molecules have evolved into large multi-cellular organisms with high metabolic rates and complex behavioural interactions. Associated with this increase there has been a transition from an asomatic, non-senescing, haploid, and asexually reproducing organism to a somatic, senescing, diploid, and sexually reproducing organism. In a few special cases there have been also an additional transition to two different forms of eusociality.

It has been shown that this directional increase in complexity is the evolutionary process to be expected in a stable environment (Witting, 1997). One essential component is selection by density dependent competitive interactions, and it is explained how this process can be integrated with the classical theories in order to obtain a general theory of evolution.

Witting, L. 1997. A general theory of evolution. Peregrine Publisher, Århus. http://www.peregrine.dk

The mobile group II introns in the mitochondrial genome of the fission yeast *Schizosaccharomyces pombe*

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The mitochondrial genomes from different strains of *Schizosaccharomyces pombe* contain up to three mosaic genes. The gene encoding the first subunit of cytochrome c oxidase (*cox1*) contains 2 introns of group I with reading frames and, in some strains, two additional group I introns without reading frames. In the minority of strains, the gene encoding cytochrome b (*cob*) harbours a group II intron. For this intron we could demonstrate that it is able to move into intronless allelic forms of the *cob* gene (intron homing) (1) and to transpose to various non-allelic locations in the mitochondrial genome (intron transposition) (2).

Recently, we could identify a group II intron in the *cox1* gene and another intron of this group in the gene encoding subunit II of cytochrome oxidase (*cox2*). In this gene, group II introns have only found in liver moss, but never in fungi.

In this contribution we present a functional analysis of the intron-encoded proteins and a characterization of the two novel group II introns.

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(2) Schmidt, W. M., Schweyen, R., J., Wolf, K., Mueller, M. W. (1994) Transposable group II introns in fission and budding yeast. Site-specific genomic instabilities and formation of group II IVS plDNAs. J. Mol. Biol. 243:137

Population differentiation of *Plantago major*

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Plantago major is an almost cosmopolitan and highly selfing species in which two subspecies are recognised, namely *major* and *pleiosperma*. The two subspecies differ in their ecology, in several morphological characters and in the allele frequencies of two allozyme loci. Within each subspecies several ecotypes can be recognised and almost each population is slightly different morphologically and has life histories that are well adapted to its habitat.

We surveyed 37 *P. major* populations from the UK, Europe and the US, including populations of both subspecies. Most populations were previously screened for their ozone resistance and showed a wide range of resistance levels. We used allozymes, RAPD and anchored inter-SSR PCR primers to survey the level of variation within the species and the differentiation of the populations.

A few new allozyme alleles were found in south European populations, but in general the allozyme data confirmed earlier results of Van Dijk et al. Compared to the allozyme data we had expected to find higher levels of population differentiation using RAPDs and inter-SSR PCR. Surprisingly the differentiation between the populations was much lower than expected. However, ssp. *pleiosperma* populations are much more diverged from each other than ssp. *major* are. The *pleiosperma* individuals are clearly distinguished from the *major* individuals.

Association of bands with subspecies, morphological characters and ozone resistance will be discussed.

Evolution of echinoderm body architecture: from molecules to metamerism.

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Adult echinoderms posses one of the most distinctive body architectures of any metazoan phylum: they are radially symmetrical, lack a head and brain, and possess several unique organs. Nearly every structure in an adult echinoderm is present in multiples of five, and many structures are arranged metamerically along the five body axes. Echinoderms almost certainly evolved from ancestors whose bodies contained few repeated structures. Comparative anatomy and the fossil record have provided only limited insights into the evolutionary origin of echinoderm radial symmetry and metamerism. We are currently analyzing the structure, expression domains, and interactions among several developmental regulatory genes in order to better understand how these morphological changes evolved. Many genes with conserved developmental roles in arthropods and chordates have apparently lost these roles in echinoderms, and have instead acquired new roles during the origin and radiation of echinoderms. For example, distal-less and orthodenticle are involved in the development of podia, and engrailed appears to pattern skeletogenesis. Furthermore, all of the genes we have examined are expressed in unusual spatial domains in echinoderms (including radial symmetry and left-right asymmetry). Expression of Hox genes in echinoderms provides insights into the origin of five-fold symmetry, and evidence of additional role recruitment. Our data include some of the most extensive evolutionary changes yet documented in the deployment and developmental roles known for these genes. Many of these changes appear to be related to the evolution of the distinctive body architecture of echinoderms.

Evolution of *Mus musculus castaneus* and *Mus caroli* in Taiwan

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Two species of *Mus* occur in Taiwan, one being commensal (*Mus musculus castaneus*) and the other (*Mus caroli*) aboriginal. Beginning in June 1995, we embarked on a population genetics study of the two species; consequently, a large number of mice are available to study the phenotypic and genotypic polymorphisms in several geographic populations of the respective species.

We first compare cranial morphology of the two species by principal component analysis (PCA) using 22 measurements on the skulls. This analysis includes one sample of *M. caroli* (N= 39) and 8 samples of *M. m. castaneus* (N= 9-193) from all over Taiwan. The results indicate that both cranial size and shape are different between the two species, being nicely separated by plotting the first and the second principal component axis. However, there is little intra-specific differentiation of cranial morphology in *M. m.castaneus* since the PCA plots of the eight samples (geographic populations) overlap substantially. Additionally, we investigate the variation in mtDNA sequence of *M. m castaneus* and discover a length polymorphism in the d-loop region. Currently, we are characterizing the nature of this length polymorphism by sequencing the region and intend to estimate gene flow in *M. m. castaneus* by the d-loop sequence.

Increasing rates of parasitism of the larval parasitoid *Bracon brevicornis* (Braconidae: Hymenoptera) by using kairomones and pheromones.

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The kairomonal effect of hexane extract of the larvae of *Ostrinia nubilalis* and *Sesamia cretica* on *Bracon brevicornis* adults was evaluated through olfactometer tests. The parasitoid males showed no definite response to any kairomone. Females were attracted to the kairomone of *S.cretica* more than to that of *O.nubilalis*. Highly significant effect of the sex pheromone of *O.nubilalis* on the females of *B.brevicornis* was recorded. Kairomones (hexane extracts of larvae) varied in their effect on the released *B.brevicornis* parasitoids. The kairomone of *S.cretica* increased the parasitisation from 7.74 to 17.05% while the kairomones of *O.nubilalis* and of *Spodoptera littoralis* were not significantly effective.

Spraying molasses solution (10%) on the corn stalks before releasing *B.brevicornis* parasitoids increased the rate of parasitism from 7.74 to 28.21%. The concentration of 5% gave insignificant increase in the parasitisation rate.

Intersexual benevolence among siblings: a sex ratio modifier in fig wasps?

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Fig wasps have long been used as model organisms for understanding Local Mate Competition and its effect on sex allocation bias. While most studies have assumed that males compete with one another, they have neglected male-female interactions as factors that may potentially distort sex allocation way from LMC predictions.

In this report we present results from a study of interactions between males and females of the Australian pollinating fig wasp *Pleistodontes imperialis* in *Ficus platypoda*. Initially there is scramble competition between males to access virgin females. During this time males excavate holes in female galls that are large enough for insemination to occur, but not for females to escape their natal galls. Once mating has ceased, males switch strategies and proceed to excavate females from galls. Experimental manipulation of the number of male within syconia shows that females are unable to dig their own way out of natal galls, and that female fitness is strongly affected by the number of males present. This suggests that sex allocation ratios in this, and potentially other, fig wasp species are affected not only by intrasexual competition among males but also by intersexual interactions between brothers and sisters. We discuss the consequences of such interactions.

Changes in mouse behaviour induced by *Toxoplasma gondii* don´t show an adaptive character

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The manipulation theory suggests that many parasites influence the hosts' behaviour in order to increase the probability of their transmission, i.e. the changes of the hosts′ behaviour are adaptive for parasite. The phenomenon has been studied on laboratory model of *Toxoplasma gondii* and its intermediate host - mouse. Some changes in behaviour of infected mice were observed (increased activity, decreased motor performance and neophilia). However, whether these changes are purposive or not has not been assesed. The simple explanation for this altered behavioural pattern is that this is only nonspecific byproduct of acute parasitic disease. If this is true, the peak of the behavioural shift should coincide with the peak of pathogenic symptoms of acute toxoplasmosis. We performed a battery of ethologicaltests at different time (3,6 and 12 weeks) after infection of F1 males and females (C57BL/10J x BALB/c) with *T. gondii* tissue cysts. The exploratoty behaviour of mice (measured in open field test decreased 3 weeks post infection (p.i.), i.e. at the time of culmination of symptoms of acute phase of toxoplasmosis. The increase of reaction time (measured in a hot plate test) was observed 6 weeks p.i.. However, all changes in behaviour of infected mice were only transient. No differences between infected and control mice were observed 12 weeks p.i.. Our results suggest that the changes in the behaviour of infected mice are nonspecific product of the acute disease rather than specific product of manipulatory activity of the parasite and that they aren´t adaptive.

Genetic variability within and among populations of the threatened foliose lichen Lobaria pulmonaria (L.) Hoffm. in Switzerland

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Lobaria pulmonaria is a foliose lichen growing mainly on beech and sycamore maple and considered as a critically endangered species in Switzerland and throughout Europe. The number and size of populations in lower elevations of Switzerland have decreased tremendously during the last decades. The remaining small populations are widely separated from each other and are presumed to be more sensitive to ecological changes and more vulnerable to extinction due to loss of genetic variation.

In this study we investigate the genetic variability of six populations of L. pulmonaria in the lowland, the pre-alps and the Alps in eastern and western Switzerland. In each population 10 to 30 thalli fragments have been sampled, depending on the population size. By PCR-sequencing of the nuclear ribosomal large subunit and the internal transcribed spacer we could distinguish seven different genotypes. A weak correlation has been found comparing genetic similarity and spatial distances between the populations. No correlations are found between genetic variation and population size. But populations having apothecia (the fruiting bodies of the fungal symbiontic partner) are significantly more variable then populations without fruiting bodies.

Genetic variability is considered as an important factor for long-term survival of a species, particularly in changing environments. Therefor we suggest to give populations having fruiting bodies a higher rank on a conservation priority list.

ZOTOV V. Wed 27 Aug P15 V. ZOTOV

he medical biologic consequences of the Chernobyl nuclear power disaser and the ways of these consequences liquidation.

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The International Scientific Information Center for Diagnostic and Rehabilitaion of the persons victimized of industrial influences.252039, Kiev, Ukraine, 0-letia Oktyabrya av. 59-a.

For the time the researches have been held, there was used for the first ime the system structural approach to quantitative investigation of the remote medical- biologic, radio- biological and radio-ecological consequences of the Chernobyl nuclear power disaster. It was revealed, that the chronic irradiation by minor dozes of radiation, which is radiated from the environment, polluted by with radioactive substances, conduces to accumulative effect which causes considerable deterioration of the inhabitants health , genetic alterations and reduction of organism resist capacity against various inauspicious influences of surroundings.

For elaboration and realization of the measures concerned to inhabitants protection of the Chernobyl nuclear power disaster consequences the following things are necessary to implement: 1.Conduct of complex medical biologic monitoring in the unified methodological basis; 2.Creating of united data and knowledge bank for the information analytic system in field of medical biologic, radio-biological and radio-ecological consequences of the Chernobyl nuclear power disaster. The object of this action is: a).situation prognostication and preventive estimate of risk for human health, issued from affected ecological systems; b) scientific basing of the most efficient contra-measures system, which permit to decrease and reduce negative consequences of the Chernobyl disaster, which exert influence upon human health and ecological systems condition (means to reduce the doze loading on human organism, prevention of the chronic irradiation by minor dozes remote consequences in combination with various chemical contaminating substances, and to diminish collective dozes for inhabitants of Ukraine to the possible minimum);

c) elaboration of scientifically based recommendations for administrative decisions taking in staff and extremal situations.

Ornament expression and immune status

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Although many models of sexual selection predict that females choose mates of high quality to pass on superior fitness to their offspring, a practical definition of that quality remains elusive. Because parasites and pathogens are virtually universal threats to animals, resistance to disease, or immune system competence, has been invoked as an ideal criterion to be used by females in mate choice. What information can a female obtain about immune function from a prospective mate's ornamentation? Most of the few studies to date suggest that males with more highly-developed secondary sexual characters produce their ornaments at the expense of immune function, so that males with redder skin patches, for example, have fewer lymphocytes. Other work has found that different aspects of immunity show trade-offs at different times of the year, with cell-mediated immunity enhanced during periods of intense sexual competition. The relationship between morphology and immune function is complex, with some traits expected to be negatively correlated with certain aspects of immunity but not others.

How shall we best measure immunocompetence to obtain a comprehensive picture of an animal's ability to resist disease? Ideally, both humoral (antibody-mediated) and cell-mediated immunity should be assessed, because immunocompetence is not a single trait. Behavioral ecologists should be wary of measuring one or even a few aspects of immunity and using those as universal gauges. Like behavior, the actions of the immune system are context-dependent, making generalizations about the function of particular components difficult unless the current and past exposure of animals to disease, their nutritional state, and other variables are known.

Effective size and *F*-statistics of a subdivided population in the finite island model

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Many organisms are arrayed into complexes of breeding units or subpopulations due to intrinsic factors, such as behavioral segregation, or extrinsic factors, such as geographic distance and habitat fragmentation. In this paper, I have derived formulae for effective size and F-statistics for a dioecious diploid population subdivided into an arbitrary number of subpopulations with migration in the island model. Stable population size and structure, discrete generations, autosomal inheritance and the island migration model are assumed, and arbitrary distributions of the numbers of male and female progeny per family, different numbers of individuals of separate sexes per subpopulation, variable migration rates of males and females are incorporated in the derivation. Some published equations for effective size and F-statistics for a subdivided population are shown to be incorrect because several incorrect probabilities are used in the derivation. A correct and more general equation for effective size is obtained by finding eigenvalue solutions to the recurrence equations for inbreeding coefficient and coancestry, which, for the special case of Poisson distribution of family size, reduces to

$$N_e = 4smfN + \frac{s(1-d_m)(1-2d_m+d_f)f + s(1-d_f)(1-2d_f+d_m)m - 1}{\frac{1}{2}(d_m+d_f)(4-d_m-d_f)},$$

where s is the number of subpopulations, $m(f)$ is the proportion of males (females) in a subpopulation of size N, $d_m(d_f)$ is the male (female) migration rate. When s=1 (a single unsubdivided population), the above equation reduces to WRIGHT's classical formula $N_e = 4mfN$ approximately. Our general expressions for F-statistics also reduce to the classical results of WRIGHT's infinite island model and its extensions. Because of the ubiquity of population subdivision and migration and their importance in determining effective size and F-statistics, population structure should be recognized and incorporated into programs for genetic conservation and evolution.

Sperm length is a sex-linked quantitative trait in the yellow dung fly Scathophaga stercoraria (L.)

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Sperm competition in the yellow dung fly is one of the classical examples in behavioural ecology of the usefulness of the optimality approach. However, the traits of sperm which influence the outcome of sperm competition are unexamined, as are potential responses to natural or sexual selection for the traits. Male yellow dung flies vary consistently in the lengths of sperm they produce. I will show that, in competition, longer sperm are more successful than shorter ones at reaching the spermathecae, from which sperm will later be used for fertilisation. A three generation heritability experiment was conducted to test the hypotheses that sperm length is at least partially genetically determined and that the determination is sex-linked.

Sperm length was significantly heritable from father to son with h^2 estimates of around 0.65, depending on the comparison used. A significantly higher heritability was estimated from the relationship between the maternal grandfather and his grandsons, giving an estimated 20% of the total variance attributable to variation on the sex chromosomes, i.e. almost all the variation in sperm length was genetically determined.

There was a significant non-linear component of the sex-linked determination. This reflects an epistatic interaction between the sex chromosome and the autosomes such that sperm length was increased when the father's sperm length would otherwise have led to the production of sperm below the mean length of those of the whole population. Sperm length is thus a male trait related to fitness and has the genetic variation necessary to respond to selection.

WEBBERLEY K.M.   Mon 25 Aug   S4   K.M. WEBBERLEY

Lack of evidence for parasite mediated sexual selection in ladybirds infected with a sexually transmitted parasite.

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Sex allows the maintenace of a wide variety of host resistence genes in a population and mating provides individuals with an opportunity to choose mates with the best parasite resistance genes. However, mating also provides ideal means by which parasites may be transmitted.

The influence of parasites on mating systems has been well considered. For example, the existence of a sexually transmitted parasite is likely to lead to selection for reduced promiscuity and mating preferences for uninfected partners. However, the majority of empirical work on parasite mediated sexual selection has centred on vertebrates. In contrast, knowledge on the influence of STD's on insect mating systems is limited.

Coccipolipus hippodamiae is a sexually transmitted parasite of *Adalia bipunctata* (two spot ladybird). Infection with this parasitic mite reduces female host fertility to zero after a few days. Given this large deleterious effect and the extremely high prevalence of the mite in certain populations (up to 89%), we would expect adaptations in the host to avoid or resist the effects of the mite, including mating preferences for uninfected partners.

Paired sib mating tests were carried out under constant temperature and humidity conditions to investigate the effect of *C. hippodamiae* infection on the mating success of both male and female *A. bipunctata*. No evidence was found for the existence of mating prefernces for uninfected partners, or indeed any connection between infection and mating success, in either sex. Possible explanations for these unexpected findings are given.

The dimensions of selection on plant resistance: thinking beyond phytochemistry.

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Thinking on the evolution of plant resistance to herbivory has been dominated by considerations of allocation to secondary chemical production. Although the allocation problem will be an essential element in any final understanding of plant defense evolution, there is much additional interesting biology to be explored. There are many ecological and physiological factors that will determine how the concentration of a particular phytochemical maps onto plant fitness. Of the many biotic features that can affect this mapping, three will be illustrated from work on *Solidago altissima* (goldenrod) and *Brassica rapa* (wild mustard). First, many insect species will respond to the general growth vigor of their host plant. When this is so, resistance to herbivory may evolve as a correlated response to other selection pressures on plant growth. Second, the threat of damage will depend on insect population density. In real communities behavioral and demographic responses by insects to their own density can curb the potential selection pressure they place on plant defense. Finally, one of the selective advantages of resistance can come through the superior competitive ability of an undamaged individual over a damaged one. This influence on competitive ability can exert a positive frequency-dependent advantage on resistance. Thus the functional relationship between chemical concentration and fitness is likely to be multidimensional. An important task of empiricists over the next decade will be to determine which of these dimensions are important to incorporate in a general understanding of defense evolution, and which are not.

he spread of agriculture in Eurasia as revealed y mtDNA sequences

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mtDNA sequences were determined from 19 ethnic groups in Eurasia. For each dataset we inferred the most appropriate model of population history using a statistical test based on coalescent theory. Moreover, we estimated the time back to the most recent common ancestor (mrca) for each population, separately. The analysis suggests a correlation between subsistence strategy and population history. Seven out of eight datasets from population that do not live on agriculture are consistent with a model of constant population size. Contrary, 11 out of 12 datasets from agricultural populations show a significant signal of population growth. In addition, the estimated times back to the mrca are clearly smaller for agricultural populations suggesting that these populations are younger.

Sex determination and genetic conflict

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There is an incredible diversity of sex determination mechanisms among plants and animals. One of the challenges of evolutionary biology is to account for this diversity, to understand the evolutionary transitions between sex determination mechanisms and to determine how selection shapes the underlying genetic structure of different sex determination systems. Here I discuss the potential role of genetic conflict in shaping sex determination systems. Conflict can occur between different genetic elements, such as cytoplasmically inherited symbionts and organelles, autosomal genes and sex-linked genes is considered. Theoretical and empirical studies are discussed, along with potential avenues for future research.

Why do drosophilid flies produce volatile aggregation pheromones when it guides parasitoids to their offspring?

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One meagerly studied aspect of the biology of *Drosophila* concerns the ecology of their communication system. Drosophilid flies produce aggregation pheromones: males produce it, transfer it to virgin females during mating, after which the female deposit it in food substrates during egg laying. These pheromones attract flies of both sexes from a distance. It is hypothesized that aggregation pheromones serve to find mates and suitable food sites. However, as these pheromones have mainly been studied by chemists that identified their chemical composition, their function in terms of costs and benefits to the flies' fitness remains speculative.

One cost became apparent only recently: The volatile aggregation pheromone is exploited by parasitoids foraging for drosophilid larvae (Wiskerke, Dicke & Vet 1993). This enables the parasitoid to track their host population which is expected to have significant consequences for host fitness and thus for the distribution and dynamics of the drosophilid population.

In this project, we aim to asses the costs of aggregation pheromone production in terms of offspring loss through parasitization. Furthermore we will study the benefit of the pheromone to the fitness of the flies by looking at its function in mate selection and resource exploitation.

The evolution of antibiotic production and resistance genes in antibiotic-producing bacteria

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The role of gene transfer in the evolution of bacteria has become an area of great interest, partly due to its importance for the evolution of antibiotic resistance in human pathogens. It has been proposed that horizontal gene transfer has also been important for the evolution of antibiotic production and resistance in soil bacteria. Phylogenetic analysis was used to evaluate this hypothesis for genes involved in the production of streptomycin and like compounds in laboratory *Streptomyces* strains. Phenotypically diverse natural isolates from an agricultural site where antibiotic production appears to be high were also examined. Molecular phylogenies based on 16S rRNA genes were compared to that for a gene from the streptomycin biosynthetic cluster. Inferences about the relative importance of gene transfer were evaluated. Further analysis of the evolution of antibiotic production involves characterization of the distribution and diversity of antibiotic production genes in a collection of phenotypically similar strains.

Estimation of incompatibility and relative male reproductive success at both pre- and postzygotic levels in the androdioecious *Phillyrea angustifolia* L.

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Androdioecy - presence of both males and hermaphrodites within a population- has been described as a rare and unlikely breeding system. In order to be maintained by selection, males must have a twofold increase in male fertility as compared to their hermaphrodite counterparts. This advantage must be even higher in a selfing population. Three species are now well-documented, among them *Phillyrea angustifolia* L. In order to examine self-incompatibility in this Mediterranean shrub and to compare male reproductive success of males and hermaphrodites, we performed two crossing experiments on plants issued from a natural population, using self, open, male and hermaphrodite pollen sources. The self pollen tube growth pattern strongly suggested a stigmatic self-incompatibility, which is corroborated by a significantly lower fruit-ratio after self-pollination. Outcross pollinations resulted in a strong pollen tube attrition, as only one tube can grow through the style to reach the ovary. The occurrence of a pollen tube within the style, considered as a potential fertility index, was significantly higher after male pollination than after outcross hermaphrodite pollination. Moreover, male pollination resulted in twice as many fruits as hermaphrodite pollination. This twofold male advantage over hermaphrodites may be sufficient to explain male maintenance within androdioecious self-incompatible populations of *Phillyrea*.

Conservation biology and multiallelic self-incompatibility systems: a story of partners and bachelors.

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A key feature of self-incompatibility (SI) systems in plants is the mate availability or proportion of compatible matings in a population. In the context of plant species conservation, it has been suggested that mate availability is generally low in small populations with multiallelic SI systems because the number of alleles maintained is expected to be low, and that this may cause a low seed set as well as a risk of extinction due to random genetic drift causing the number of alleles to decrease under some threshold value. We perform a theoretical investigation of mate availability and extinction probability in a population using different models of multiallelic SI in mutation-selection-drift balance. Four models of SI systems are compared: gametophytic self-incompatibility (GSI); sporophytic self-incompatibility (SSI) with codominance in pollen and stigma (SSIcod); SSI with dominance in pollen and stigma (SSIdom); SSI with dominance in the pollen and codominance in the stigma (SSIdomcod). The results show large differences among the SI systems in average mate availability as well as in variances of mate availability among individual plants. These differences are most pronounced in small populations. Stochastic simulations in populations with 30 individuals show that the probability of extinction due to loss of alleles is very small in case of a Poisson distribution of the number of offsprings.

As a conclusion, SI sytems may cause reduced seed set in small populations because of a limitation in mate availability, but the effect is restricted to some models of SI and to very small population sizes. However, the net effect of SI systems on fitness in small populations is difficult to assess because of the influence of SI on the effective population size and the level of inbreeding.

ne flow in fragmented populations of insect-pollinated plants.

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ecently, many plant populations have become fragmented, often due to itat destruction. The resulting small and isolated populations face an nhanced risk of extinction. As these small populations will be subjected to enetic drift and inbreeding they may experience a decrease in fitness and a oss of adaptibility. These negative genetic effects of fragmentation may be lleviated by gene flow between the remaining fragments. In the presence f sufficient gene flow, loss of genetic variation and fitness will be limited. As in many plant species dispersal of seeds is restricted, gene flow will mainly be mediated by pollen exchange. Fragmentation may affect gene flow in several ways. Not only will the distances increase between remaining patches, but the patches may also become isolated by 'physical' barriers, like hedges. In addition, insect-pollinated plants have to compete for pollinators, and these competitive relations might be affected by fragmentation. The presence of other flowering species may be either beneficial or detrimental, depending on their relative attractivity to pollinating insects.
We have studied the effects of fragmentation on gene flow by pollen for the insect-pollinated plant species, *Scabiosa columbaria*. Experimentally, we subjected small patches of *S. columbaria* to various types of isolation and determined the level of gene flow between patches. We measured both the amount of pollen transport, by directly counting pollen grains, and the efficiency of the resulting gene flow by means of allozyme electrophoresis. We systematically investigated how pollen transport and gene flow are affected by various isolating mechanisms, by the presence of other plant species, and pollinator behaviour. The results will be discussed in a conservation biological context.

VERARDI A. Mon 25 Aug S20b A. VERARDI

GENETIC STRUCTURE AND HYBRIDIZATION IN *AP* *MELLIFERA* POPULATIONS OF SARDINIA

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Apis mellifera is a highly polytypic species whose autochthonous distribution ranges from southern Scandinavia to the Cape of Good Hope, and from the West coasts of Africa to the Ural and East Iran. Its presence elsewhere is due to human importation. Morphometric analysis and molecular genetic studies permitted the characterization of 24 subspecies grouped into three clusters: A-branch with the African and South Mediterranean races, C-branch with the races from the East including the Italian *A. m. ligustica* and M-branch with the races of the West Mediterranean (*A. m. mellifera*).

In our study we analysed samples from the island of Sardinia by means of protein electrophoresis and mtDNA COI-COII intergenic region restriction site polymorphism. Three different mtDNA restriction patterns were observed overall: two, M3 and M7, previously found in populations of the *mellifera* group; one, C1, typical of populations of *ligustica* and the other races of the C branch. M lineage haplotypes were most frequent in isolated apiaries where traditional beekeping is still practised; *ligustica* colonies instead were abundant in areas of intensive and modern apiculture. At the nuclear level the samples were quite homogenous showing everywhere frequencies *ligustica*-like at two loci, *Mdh-1* and *Est-2*, otherwise differentiated between the two groups. Such a scenario could be interpreted as populations of the *A. m. mellifera* group being autochthonous in the island while those of *ligustica* origin having been imported in recent times after epidemics of Varroa had decimated local apiaries.

A highly asymmetric hybridization between the two races occured gene flow being due mainly to *ligustica* drones. This hypothesis needs to be confirmed by analysis with more variable nuclear markers like microsatellite loci.

VERBOVEN N. Mon 25 Aug C1 N. VERBOVEN

est desertion and renesting behaviour in great tits

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tudies on reproductive success in birds often focus on reproductive decisions uch as the timing of breeding and clutch size. However, in multiple brooded pecies reproductive success is often determined by the number of clutches roduced in one season. Interestingly, renesting does not only take place when he young from a previous nest have fledged. It also occurs before a current reeding attempt is finished, resulting in zero offspring from the earlier clutch. at is the reason that birds give up their current clutch in favour of a eplacement clutch? Nest desertion and renesting behaviour was examined in a acultatively double brooded population of great tits (*Parus major*). In this tudy nest desertion was experimentally induced by removing a number of eggs om the first clutch. The probability of desertion was related to the original lutch size and to the number of eggs that remained in the nest after the anipulation. The frequency of nest desertion decreased dramatically from egg aying to the end of the incubation period. By renesting great tits may produce ore recruits per season and thus increase their fitness.

Genetic structure and diversity in the endemic phytophagous beetle *Nesaecrepida darwini* on the Galápagos Archipelago

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The endemic flea beetle *Nesaecrepida darwini* is exclusively found in the coastal zone of the Galápagos islands, feeding on its host plant *Cryptocarpus pyriformis.*

Six populations from three different islands (Isla San Cristobal, Isla Santa Cruz and Isla Isabela) were screened for allozyme polymorphisms by means of cellulose acetate gel electrophoresis. A total of 12 presumptive loci were scored of which 3 were monomorphic, 4 showed less than 5% polymorphism and 5 were highly polymorphic.

Populations from Isla Isabela, the youngest island investigated in our study, showed lowest heterozygosities. This could be explained if the origin of these populations is to be found in a more recent colonisation of this island by a limited amount of individuals (founder effects), originating from nearby older Islands. At the same time these results suggest that this species may have already been present since the early evolutionary history of the Galápagos Archipelago.

Modified Rogers Genetic distances were calculated between all populations and both UPGMA and distance Wagner dendrograms constructed. The populations are grouped by island, and those from Isla Isabela are separated first. The high amount of genetic differentiation between the islands indicates that, although the species is macropterous it does not show high amounts of gene flow between the islands. Moreover, we observed a relatively high differentiation between populations from the same island, sometimes even at relatively small distances. The main reason for this might be the patchy distribution of the populations, suggesting the importance of recurrent extinctions and recolonisations on a small scale.

Phylogeography of the Galápagos flea beetle *Nesaecrepida darwini* Mutchler (Coleoptera: Chrysomelidae) based on mtDNA evidence

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Nesaecrepida darwini is a small endemic flea beetle known from several islands of the Galápagos Archipelago. It has a patchy distribution along the coastline where it often can be found in high numbers feeding on its host plant: saltbush (*Cryptocarpus pyriformis*). We analysed material from 10 localities including 7 islands of the Galápagos archipelago, differing in age and size.

Sequence variation in a 369 bp segment of the mitochondrial DNA COI gene was studied using PCR (primers: 5'GGAGGATTTGGAAATTG ATTAGTTCC 3' (C1-J-1718) and 5' CCCGGTAAAATTAAAATATAAA CTTC 3' (C1-N-2191) and automated sequencing (using ALF DNA sequencer [Pharmacia]). The sequences were aligned by eye and a tree based on Maximum Parsimony analysis was constructed using PAUP 3.1.1. As outgroup we included the Chrysomelid beetle *Ophraella arctica*.

All specimens are grouped together according to the islands on which they were collected. Island age seems to be an important factor to explain the phylogeographic pattern within this species. Nucleotide variation varies between islands. The observed pattern may be explained by separate colonisations of the different islands, the oldest islands being colonized first.

The evolution of trophical adaptation in the Tanganyikan cichlid genus *Petrochromis* (Pisces: Cichlidae) inferred from geometric morphometrics and mtDNA sequences

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Lake Tanganyika harbors almost two hundred endemic cichlid species. The relative importance of intrinsic biological factors (e.g. differentiation in behavior, morphology or ecology) and abiotic factors (such as physical barriers to geneflow) in the modes of speciation that resulted in these adaptive radiations remains controversial. With regard to ecological and behavioral divergence, morphological features related to feeding are suggested to have been important in the evolution of these species flocks.

In this context we studied the endemic Tanganyikan cichlid genus *Petrochromis* which are highly specialised algal feeders. *Petrochromis* species have a protrusible snout, tricuspid teeth with the crowns curved backwards. They differ in the degree of the relative upper jaw predominance, number of jaw teeth, arrangement and density of the jaw dentition, degree of development of the adductor mandibulae muscles and complexity of the convolution of their intestinal tract.

In order to investigate the importance of some of these morphological changes for the speciation in these fishes, we related the pattern of body shape variation - obtained from geometric morphometrics - to their phylogeny inferred from DNA sequences from the mitochondrial control region.

VERHOOG M. . Thu 28 Aug C5 · M. VERHOOG

The influence of genes for melanism on the activity of the flour moth, Ephestia kuehniella Zeller.

M.D. Verhoog, C.J. Breuker and P.M. Brakefield

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The effects of genes controlling melanism on levels and patterns of activity, which are potential non-visual components of fitness, were investigated in the Mediterranean flour moth *Ephestia kuehniella* Zeller (1879). Six genotypes of two melanic strains ('Ala nigra' and 'black') were used. The activity of 45 mated females per genotype was monitored continuously during the third night of their lives. The measurements were carried out by use of automatic electrostatic techniques.

Although there was high individual variation within genotypes, the bb (melanic) females were the most active. Moths of this genotype tended to show more bouts of activity than those of other genotypes.

Potential covariates, such as the number of fertile eggs laid or the dry weight of the females, could not explain the differences in number of activity bouts. The results are discussed in the context of industrial melanism in moths.

Energetics, immune function, and trade-offs in evolutionary ecology

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Trade-offs between fitness components are a central concept in evolutionary ecology, and the existence of such trade-offs is now well established. In recent years research effort has shifted emphasis towards trying to understand the mechanisms causing the observed patterns. Knowledge of the mechanisms mediating trade-offs is important because this may enable us to make predictions regarding the importance of a given trade-off under different environmental conditions. Using recent results from avian studies, the role of energetics and immune function in mediating effects of effort (signalling, reproduction) on fitness costs will be discussed.

PRELIMINARY DATA ON THE MOLECULAR VARIATION IN *QUERCUS ROBUR* COMPLEX FROM PENINSULAR ITALY, SARDINIA AND CORSICA

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Oaks of *Quercus* sect. *robur* Rchb. are a critical group from a systematic point of view for their high level of phenotypic heterogeneity. A large number of taxa has been described since the earliest botanical surveys, particularly from populations of the southernmost regions. However, suggested intra- and interspecific relationships still lack a satisfactory systematic framework. Similar patterns from other parts of the European ranges have been related to intense processes of hybridization and introgression (Rushton, 1993). Processes of reiterated range isolation and coalescence, triggered by the quaternary climatic fluctuations are likely to have produced a high degree of both genetic heterogeneity and gene exchange upon recontact (Ferris *et al.*, 1993, 1995). Current floristical surveys show an increasing interest in rehabilitating "old" taxa, most of them with very restricted local distribution. Their diagnostic value is then extended to larger or surrounding territories: a taxonomically unrealistic accumulation of binomia follows, affecting any consistent theory on spatial and temporal patterns of speciation in this complex. Twenty populations from locations scattered throughout peninsular Italy and surrounding islands have been examined by means of morphological and isozyme analysis. The samples analyzed belong to *Quercus robur, Q. petraea* and *Q. pubescens s.l.* populations. Allozyme variation at 16 loci (*Skdh, Mdh-1, Mdh-2, Icdh-1, 6Pgdh-1, 6Pgdh-2, NADHdh-1, Per-1, Per-2, Adk, Ap-2, Est-1, Lap-1, Gpi-1, Gpi-2, Pgm*-2) showed that only 2 are monomorphic (*Adk* and *Gpi-1*) whereas 14 are polymorphic. Polymorphisms were also detected at cpDNA level in the same populations. The overall data revealed a substantial amount of shared alleles at different loci between the considered taxa, indicating that they belong to a single syngameon. These data extend further south the conclusion drawn by Ehrendorfer *et al.*, 1995 for Austrian populations belonging to the *Q. robur* complex. Genetic data indicate that the structure of this syngameon has remained rather homogeneous over a surprisingly large area; the relatively sudden emergence of *Quercus* in pollen cores from Central Europe (Bennet *et al.*, 1991) suggests that the holocenic range recovery of the *Quercus robur* complex might have relied upon refugial areas scattered from Mediterranean districts up to the middle latitudes.

Evolution of functions of carotenoid pigments: an example of preadaptation.

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Carotenoids first emerjed in non-photosynthetic bacteria as lipids reinforcing cell membranes. To serve this function their long molecules have extremely rigid backbone due to the linear chain of usually 10 to 11 conjugated C=C bonds - the length corresponding the thickness of hydrophobic zone of membrane they penetrate as "molecular rivets". Carotenoids retain their membrane-reinforcing function in some funghi and animals.

The general structure of carotenoid molecule, originally having evolved in bacteria for membrane reinforcement, posess a number of other properties that were later realised as independent functions in other taxa. The most striking fact is that these properties proved to fit some new functions to perfection.

- Polyene chain of 9-11 double bonds absorbs light in the gap of chlorophyll absorption - function as accessory light-harvesting pigments in all plants;
- Polyene length of 9 conjugated bonds is shown to be the minimal one for quenching singlet oxygen and effective elimination of dangerous radical species - antioxidant function in great variety of organisms.
- Unique arrange of electronic levels endowed by polyene makes carotenoids the only natural compounds capable of excitation energy transfer both i). from carotenoid excited state to chlorophyll in light-harvesting complex and ii). from triplet chlorophyll or singlet oxygen to carotenoid in photosynthetic reaction centers - protection of RC from photodamadge.

Carotenoids have many other biological functions, among them: specific coloration in plants and animals, light-screening, defence of egg proteins from proteases in some invertebrates; immediate carotenoid derivative - retinal - acts as photoreceptor pigment in vision and in bacteriorhodopsin photosynthesis, retinol in animals and abscisic acid in plants serve as hormons. All these functions utilize various properties (mechanic, electronic, steric) of a single structure - linear polyene chain evolved in bacteria for a single membrane-reinforcing function, thus demonstrating a clear example of preadaptation.

Plasticity in body shape of *Daphnia galeata* in response to *Perca* and *Chaoborus* kairomones: a morphometrical study

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Abstract

Laboratory life table experiments were used to study the responses of two clones of *Daphnia galeata* to kairomones from a fish (*Perca*), from an invertebrate (*Chaoborus*) predator and from a mixture of both kairomones. The body shapes of daphnids in their sixth adult instar were analysed with a morphometrical tool. The main result was that daphnids exposed to the *Chaoborus* kairomone had a significantly larger body (length and carapace width) than the animals from the treatments with *Perca* kairomone or the kairomone mix. Additionally, the daphnids from the *Chaoborus* treatment featured an extremely pointed rostrum. In the *Perca* treatment a significantly wider head and a smaller eye were produced. When exposed to both the kairomone the animals mostly resembled the *Perca*-cue exposed individuals. In general the biggest differences were found between the shape of *Daphnia* induced by the *Chaoborus* cue as compared to all other treatments. by assuming a rather triangular shape with a broad carapace and a narrow, long head. The daphnids exposed to *Perca* kairomone, on the contrary, more closely approached the form of an ellipse. This could be of importance for their successful escape from predation and hydrodynamic abilities.

Population genetics of subdivided plant populations with a seed bank.

Renaud VITALIS and Isabelle OLIVIERI

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Since Wright's seminal work, spatial structure is known to affect the genetic distribution of genes in populations. Descriptors such as effective size, as well as *F*-statistics have been extensively used to account for the effect of population subdivisions on genetic drift and inbreeding. On the other hand, the effect of age structure of individuals has been studied, but only in the case of finite isolated populations. However, in natural populations, it is obvious that both effects take part in the distribution of genetic variation. Monocarpic perennial plants, as well as plant species with a seed bank are such examples. Only verbal arguments exist that suggest the seed bank could constitute a reservoir of diversity. We propose an analytical model of population structure with a seed bank. This model could also describe any species with an age-structured life stage that do not disperse. We investigate the effects of both spatial and temporal structure on effective size and equilibrium values of *F*-statistics.

ize dependent male reproductive success in a wind llinated plant.

laas Vrielin [1,2], Joël Cuguen[1], Pierre Saumitou-
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Total plant fitness can be divided in two components: fitness obtained through male and female function. The contribution of both functions to total fitness may to vary with plant size. With regard to male function in wind pollinated plants in general three types of fitness gain curves are proposed. If pollen is distributed homogeneously and over large distances male fitness is expected to increase linearly with plant size. Burd and Allen (1988), however, proposed an accelerating gain curve with plant size. They argued that if plants are larger they will become taller which would facilitate dispersion of pollen and therefore male fitness would increase more than linerly with plant size. Finally the fitness gain curve could be decelerating with plant size. This could be the case if pollen dispersal is inhomogeneous and frequently over short distances, so that large plants saturate stigmas of the neighbours with pollen.

We tested which of these shapes applied to the wind pollinated herb *Beta maritima*. We measured male and female fitness of *B. maritima* in a small artificial population with plants differing in size and architecture. Male fitness was measured through paternity analysis of seeds with DNA fingerprinting and RFLPs. Male fitness in *B.maritima* was positively correlated with female fitness and decelerated with plant size.

WALDMANN P. Wed 27 Aug P13 P. WALDMANN

Relationships between heritability of fitness characters, allozyme heterozygosity and population size in the rare plant *Scabiosa canescens* W.&K. and its congener *S. columbaria* L.

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We quantified levels of genetic variation in six populations of varying size of th rare and ecologically restricted plant *Scabiosa canescens* (Dipsacaceae, 25 populations in southern Sweden) and the more common congener *S. columbari* (100 populations in the same region) to see whether the heritability of quantitative traits was related to allozyme diversity and population size. The number of flowering individuals per population ranged between 25 and 5000 for *S. canescens*, and between 55 and 5000 for *S. columbaria*. Mean allozyme heterozygosity (five loci for *S. columbaria* and two loci for *S. canescens*) were estimated on the basis of 25 individuals per population Broad sense heritabilitie (H^2) were estimated for leaf number, maximum leaf length, area of longest leaf, first flowering date, height of central stem, maximum plant height, number of heads and flower size, in a greenhouse, based on 25 maternal families per population. There were no significant correlations between population size and expected heterozygosity (H_e). Estimates of H^2 varied independently of H_e in bo species, the only exception being leaf area in *S. canescens* ($r = 0.78$, $P < 0.05$). H^2 was negatively correlated with population size for leaf area, leaf length and flower size ($r = -0.65$, -0.67 and -0.67, respectively, $P < 0.05$) in *S. columbaria*, and with flowering date ($r = -0.72$, $P < 0.05$) in *S. canescens*: the only significant positive association with population size involved H^2 for leaf number in *S. canescens* ($r = 0.777$, $P < 0.05$). Hence, this study demonstrates that small population size not always leads to a reduction in genetic variation and that the level of allozyme variation seems to be a poor predictor of the amount of genetic variation in the majority of quantitative characters.

Congress ESEB97 Programme version 19 Aug 97

Sat 23

Changes in Authors, their Positions and in Rooms are in **GREY HATCHED BOLDFACE**

14:00-22:00 Arrival and registration

20:00-22.00 JEB Editorial Board **in Room 10k+l**

Sun 24	6+7	8+9	**4+5**	12+13	11
8:30-9:30				Brakefield	
	Evolution of Sexual and Social Systems	**Coevolutionary Interactions**	**Adaptation and Fitness**	**DNA and Evolution**	**Selection, Drift, and Evolution**
9:35-9:40	**S2 Sex determinatior**	**S8 Plant-Herbivores**	**S12 Plasticity**	**S20 Geographical pa**	**S24 Organism and M**
9:40:10:10	Bopp	Mattson	Dorn	Hewitt	Gorshkov, Victor
10:10:10:40	Werren	Strauss	Van Tienderen	Bachmann	Laland
coffee					
11.10-11:40	Saumitou-Laprade	Tuomi	Pigliucci	Nichols	Syvanen
11:40:12:00	Mittwoch	Weis	Sultan	Lenormand	**Alekhina**
12:00-12:20	Kraak	Honkanen	Ottenheim	Nuernberger	Bulat
12:20-12:40	Antezana	Marak	Smekens	Mueller	Makarieva
lunch	12:45 -14.00 Meeting Council & Officers 1 in **Room 10k+l**				
14:10-14.30	Rigaud	Janz	Gabriel	Cosson	Filatov
14:30-14:50	Beye	Egas	Van Straalen	Cianchi	Òtto
14:50-15:10	Butcher	Kooi	Ernsting	Grandjean	Lenton
15:10-15:30	Gertsch	Biere	Martinez	Fedorov	Gorshkov, Vadim
15:30-15:50	Krieger	Desouhant	Repka	Alberch (Boto)	Sokolov
tea		**C2 Animal life h.**			**C4 Applic Molecular**
16:20-16:40	Van Dijk P.	Toupance	De Jong G.	Salemi	Gonzales-Candelas
16:40-17:00	Dikalova	Reuter	Gibert	Vandamme A.M.	Procaccini
17:00-17:20	De Jong T.	Johst	Roskam	De Haan	Launey
17:20-17:40	Vassiliadis	Spaak	Windig	Wolff, Kirsten	Desmarais
17:40-18:00		**Fjerdingstad**	Wijngaarden	Dijkstra	Souty-Grosset
dinner					
20:00-20:45				Stearns, Presidential Address	
20:45-21:30				Anstett, JMS lecture	

Mon 25	6+7	8+9	**4+5**	12+13	11
8:30-9:30				Lenski	
	S4 Sexual selection	**S9 Symbiosis**	**S11 Plant life historic**	**S18 Microsatellites**	**S21 Conservation**
9:40:10:10	Zuk	**Moya**	Cohen	Pollock	Lande
10:10:10:40	Moller	Law	Schlichting	Ruiz Linares	Arctander
coffee					
11.10-11:40	Grahn	Douglas	Savolainen	Feldman	Avise
11:40:12:00	Kotiaho	Hackstein	Prus-Glowacki	**Garza**	Bijlsma
12:00-12:20	Bakker	Van Hoek	Mathias	Falush	Van Oosterhout
12:20-12:40	Alatalo		Klinkhamer	Perrin	Gaggiotti
lunch	12.45-14.00 Meeting Council & Officers 2 in **Room 10k+l**			**S20b Geographical p**	
14:10-14.30	Kokko	Van Ham	Ronce	Pongratz	Van de Zande
14:30-14:50	Webberley	De Vries	Piquot	Gerace	Saccheri
14:50-15:10	Parri	Breeuwer	Engel	Bjorklund	Nielsen
15:10-15:30	Hovi	Van Alphen	Atkinson	**Serra**	Santucci
15:30-15:50	Siva-Jothy	Bouchon	Vrieling	Kuusipalo	Vekemans
tea	**C3 Plant reproductio**		**C1 Bird Life History**		
16:20-16:40	Meiser	Van Meer	Fauchald	Van Moorsel	Edmans
16:40-17:00	Velterop	Schilthuizen	Pulido	Verra	Siikamaki
17:00-17:20	Smithson	Scudo	Doutrelant	Brunton	Kuitinnen
17:20-17:40	Ferdy	Gibernau	Verboven	Post	Fischer
17:40-18:00	**Rademaker**	Gaume	Gavrilov		Hauser T.
18.15 dinner					
19:30-20:15	Plenary ESEB Business Meeting				
20:30-22:30	**Workshops W1 / W7**				

Tue 26	6+7	8+9	4+5	12+13	11
8:30-9:30				Akam	
9:35-9:40	**S1 Heteromorphism**	**S10 Genetic Conflict**	**S15 Microbial Evolut**	**S17 Modular vs Segn**	**S23 Domestication**
9:40:10:10	Till-Bottraud	Tristem	Riley	Dick	Kruska
10:10:10:40	Fenster	Nuzhdin	Chao	Spring	Ferrand
coffee					
11.10-11:40	Sachs	Ardlie	Dorit	Wray	Le Thierry d'Ennequin
11:40:12:00	Ressayre	Andersson	Blot	Boero	Allaby
12:00-12:20	Mignot	Hurst L.	Kulakov	Cook C.E.	Poncet
12:20-12:40	Joly	Cook J.M.	Rainey	Minelli	Tiedemann
12:40-13:00		McVean			
lunch					
13.45 -			**Excursions**		

Wed 27	6+7	8+9	4+5	12+13	11
8:30-9:30				Jackson	
9:35-9:40	**S5 Reproductive isol**	**S6 Parasite-host**	**S13 State-dependent**	**S16 DNA evolution**	**S25 Major Transition**
9:40:10:10	Hollocher	Richner	Shanley (Kirkwood)	Excoffier	Szathmary
10:10:10:40	Arnold	Agnew	Mace	Harding	**Roze** (Michod)
coffee					
11.10-11:40	Tregenza	Lafferty	Verhulst	Sajantilla	Keller
11:40:12:00	Seehausen	Hochberg	**Lumma**	Schluens	Freeland
12:00-12:20	Aanen	**Shykoff**	Cadee	Weiss	Bengtson
12:20-12:40	Trouve	Pomiankowski	Prevot-Julliard	Austerlitz	Brookfield
lunch					
14:10-15:00			**Parallel Poster sessions P1 / P16**		
15:00-15:50					
tea	15.30 Film Joly and	**film Thiel**			
16:20-16:40	Kirkpatrick	Clay	Kozlowski	Nielsen	Kobayashi
16:40-17:00	Rolan Alvarez	Bauchau	Cichon	Chevillon	Noest
17:00-17:20	Michalak	Nash	Gotthard	Giessler	Sella
17:20-17:40	Ferguson	Flegr	Julliard	Barome	Witting
17:40-18:00	Schwarz (Leijs)	Rolff	Buckling	Aguade	Boxma

Conference dinner

Thu 28	6+7	8+9	4+5	12+13	11
8:30-9:30				Piersma	
9:35-9:40	**S3 Cooperation**	**S7 Parasitic diseases**	**S14 Genet. fitness**	**S19 Exon-Intron**	**S22 Drift in natural p**
9:40:10:10	Komdeur	Levin	Keightley	Cerff	Charlesworth
10:10:10:40	De Waal	Koella	Chapman	Go	Barrett
coffee					
11.10-11:40	Ratnieks	**Kover**	Travisano	Stoltzfuss	Whitlock
11:40:12:00	Greeff	**Van Baalen**	Turner	Dewilde	Kraft
12:00-12:20	Sundstrom	Kaltz	Korona	Hankeln	Caballero
12:20-12:40	Beekman		Kammenga	Matthews	Palsson
lunch					
14:10-14.30	Seppa	Kraaijeveld	Davies	Da Lage	Giles
14:30-14:50	Heinze	MacKinnon	Leroi	Wolf, Klaus	Vitalis
14:50-15:10	Peeters	Slade	Betran	Haring	Armbruster
15:10-15:30	Sterck	Taskinen	Matos	Harlid	Wang
15:30-15:50	**Thiel**	**Pijls**	Azevedo	Torti	Lenfant
tea		**C6 Predators/parasit**		**C5 Animal T/O**	
16:20-16:40	Hogendoorn	Bot	Blanckenhorn	Ahlroth	Schierup
16:40-17:00	Thoren	Pels	Ward	Crnokrak	Staedler
17:00-17:20	Pedersen	Frischknecht	Guillemaud	Verhoog	Gandon
17:20-17:40	Neumann	Jansen	Sabelis	Mappes	Heyer
17:40-18:00	Lachmann	Driessen	Lesna	Nordeide	Hardy
dinner					
Farewell party					