

# biology09

12-13<sup>th</sup> February 2009

zoology

University of Bern and Natural History Museum Bern  
Charles Darwin's 200<sup>th</sup> Birthday  
150 years „Origin of species“

botany

**Abstract book of talks**

mycology

Uni S - room A003

**Invited speakers...**

Clive Brasier

Fredrik Ronquist

Nina Wedell

James Bullock

John Pannell

systematics



Institute of Ecology  
and Evolution -  
University of Bern



Natural History  
Museum Bern

## **Walking with plants: the ecology of seed dispersal**

*James Bullock, NERC, Centre for Ecology & Hydrology, Oxon*

Plant dispersal research has advanced hugely over the last few years. In this talk I will discuss some of these advances using my own research for illustration. This involves combining empirical and modelling approaches, the latter including mathematical and simulation models. Dispersal is clearly critical in a plant's life cycle and this is confirmed by evidence of complex adaptations. These include the archetypal ant-seed interaction, but there is recent evidence of less obvious adaptations such as abscission velocities in win-dispersed seeds. Despite evolution, we are also realising the immense importance of non-standard dispersal mechanisms, whereby seeds are dispersed by vectors to which they are not clearly adapted. For example, our work is providing the first quantifications of seed dispersal by humans; showing humans may take seeds orders of magnitude further than other vectors. We are also addressing explicitly the role of dispersal in a plant's life cycle. Recent advances in spatial population modelling provide plant ecologists with tools to integrate dispersal with population ecology. Analytical invasion models are relatively easy to use and are remarkably accurate despite their simplicity. We are also developing metapopulation models which are more realistic and relevant to a plant's life-cycle than current models. The new models show that the tail of the dispersal kernel is critical in governing patterns and rates of spatial dynamics, and so methods are being developed to quantify this tail. I give examples of novel approaches to mechanistic modelling and empirical measurement and suggest future directions for dispersal research.

## **Female Zebra finches increase their sons' attractiveness through extra-pair copulations: a cautionary tale**

*Barbara Tschirren*

Extra-pair copulations are common in most bird species and have obvious fitness benefits for males. For females, however, the benefits are less clear but might include indirect genetic benefits (i.e. good genes) for their offspring. Indeed there are a number of studies showing that offspring sired by extra-pair partners have a greater viability and are more sexually attractive than their within-pair siblings. Here, I present a study on Australian Zebra finches, in which I identified a colour ornament that is both under sexual selection and highly heritable in two populations with a different selective background. Hence, females could obtain genes for increased offspring attractiveness by engaging in extra-pair copulations with highly ornamented males. Indeed, I observed larger ornaments in sons sired by extra-pair partners, seemingly supporting the good gene hypothesis. However, when comparing the ornament size of within-pair and extra-pair partners, there was no difference. Thus, environmental effects, such as differential maternal allocation of resources in eggs fertilized by extra-pair males, must have led to the observed differences in ornament expression. Indeed, I found evidence that maternal investment in egg size is associated with ornament expression in sons. Hereby, this study demonstrates that maternal effects can critically shape sexual selection by altering the genotype–phenotype relationship of ornament expression in offspring. It also cautions against automatically attributing greater offspring attractiveness or viability to a male's heritable genetic quality, as without controlling for differential maternal investment, we may significantly overestimate the role of indirect genetic benefits in the evolution of extra-pair matings.

## **Origin of Cyanobacteria: Was the most common ancestor multicellular?**

*Bettina E. Schirromeister*

Multicellularity is commonly viewed as one of the major transitions in the history of life that have increased complexity. The origin of multicellularity in eukaryotes is well studied whereas useful data within prokaryotes are still limited. Cyanobacteria are one of the few prokaryotic phyla where multicellularity has evolved. Cyanobacterial fossils have been dated 2,700 Ma, with multicellular forms as early as 2,450 Ma. Understanding the evolution of multicellularity in these old bacteria will give insights into the early history of life. We conducted and compared phylogenetic analysis of 16S sequences from prokaryotic cyanobacteria and 18S rDNA sequences from eukaryotic chlorophyta. These analyses indicate that in the case of cyanobacteria the base of the phylogenetic tree is exclusively occupied by multicellular species. Ancestral character state reconstruction suggests that the most common ancestor of all extant

cyanobacteria was multicellular. It also shows that bidirectional transitions between multicellular and single-celled forms are common in the prokaryotic cyanobacteria. Our analyses indicate that losing and regaining multicellularity is relatively easy within a phylum, which raises the question whether evolving multicellularity is as difficult as commonly assumed. Furthermore the multicellular ancestry of cyanobacteria raises the possibility that the origin of life was more extensively dominated by multicellular organisms than generally assumed.

## **Separating genotypic and environmental variation in specific leaf area in a widespread Alpine plant**

*J.F. Scheepens, E. Frei, J. Stöcklin*

Specific leaf area (SLA) is one of the mostly used plant functional traits as it is an indicator of, for instance, relative growth rate, stress tolerance or leaf longevity. Aside from interspecific variation in SLA, substantial intraspecific variation exists, which usually correlates with environmental conditions. This intraspecific variation may have a genetic component, but may also result from phenotypic plasticity. To successfully predict species responses to environmental change, it is important to estimate phenotypic plasticity in SLA. We separated genotypic and environmental components of SLA in leaves of the widespread Alpine bell flower *Campanula thyrsoidea* after transplantation to three common gardens along an altitudinal gradient (600m, 1200m and 1800m a.s.l.). Before transplantation, the plants were grown from seeds which were gathered from 16 populations in four Alpine biogeographic regions corresponding to phylogeographic groups. After transplantation, plants immediately replaced their leaves, and ten weeks later we measured SLA from mature leaves. We found that SLA decreased with altitude, suggesting adaptive phenotypic plasticity. However, SLA values increased with increasing altitude of origin, indicating a strong genetic adaptation of SLA to altitude. The four Alpine regions were differentiated, indicating a phylogeographic effect in accordance with postglacial migration history, although adaptation to unknown environmental factors cannot be excluded. We speculate that phenotypic plasticity in SLA allows individuals to colonize new habitat. Over longer time periods, the population-wide SLA adapts genetically to the new environmental conditions. Therefore, intraspecific variation in SLA and its plasticity rather than single SLA values should be preferred in vegetation models.

## **Evolution of metabolic networks: Robustness and Innovation**

*João F. Matias Rodrigues and Andreas Wagner*

Genome-scale metabolic networks are known to be highly robust to elimination of enzyme-coding genes. However, beyond the effect of single or double mutations little is known about the evolution of these large metabolic networks which can evolve rapidly through eliminations of enzyme-coding genes and also through horizontal gene transfer that adds new enzyme-coding genes. The use of computer simulations allowed us to study a vast space of metabolic network genotypes that would otherwise prove unmanageable. In this project we studied how metabolic phenotypes change with the metabolic networks, here we define phenotype as the ability to sustain life in an environment in which a certain spectrum of carbon sources is available. We show that metabolic networks can, through single mutations, become very different final metabolic networks while still preserving their metabolic phenotype. This plasticity of metabolic networks is important for innovation because it allows metabolic networks to evolve without change of phenotype and therefore increase the number of different metabolic networks with different phenotypes that are encountered, thus increasing the chances of finding a more fit phenotype. Additionally, we find that two metabolic networks with the same phenotype have few essential reactions in common and also that the robustness of the *E. coli* metabolic network to mutations is typical of networks with the same phenotype. Finally, we find a set of reactions that are essential to all metabolic networks which could be ideal targets for antibacterial drug design.

## **Social transfer of fungal resistance in ants**

*Anabelle Reber, Michel Chapuisat*

The huge ecological success and complex social life of ants request efficient defences against parasites. Recent findings suggest that group diversity improves the mean resistance of ants challenged with entomopathogenic fungi. Better disease resistance in groups probably results from the transfer of resistance among group members, for example by sharing endogenously-produced antibiotics or when the behaviour of some specialists protects other individuals. Moreover, the diversity in parasite resistance may be of genetic or environmental origin. In this study, we experimentally tested if a transfer of resistance occurred (1) between genetically diverse ants and (2) between ants that differed in their past exposure to a fungal pathogen. In a first experiment, we found that the survival of *Formica selysi* workers challenged with *Beauveria bassiana* was improved in presence of an ant from another genetic lineage. The transfer of resistance occurred only if ants were still in contact after infection, which suggests a curative behaviour. In a second experiment, we found that the survival of a naïve ant (without previous contact with the parasite) was improved after a contact with a previously immunized ant. This social transfer of resistance occurred before infection and may thus have a prophylactic effect. Transfers of resistance may play a prominent role for disease protection in colonies of social insects that are characterized by division of labour and often contain multiple breeders.

## **The evolution of judgement bias in indirect reciprocity**

*Rankin, D.J. & Eggimann, F.*

Indirect reciprocity is a form of reciprocity where help is given to individuals based on their reputation. In indirect reciprocity, bad acts (such as not helping) reduce an individual's reputation while good acts (such as helping) increase an individual's reputation. Studies of indirect reciprocity assume that good acts and bad acts are weighted equally when assessing the reputation of an individual. As different information can be processed in different ways, this is not likely to be the case, and it is possible that an individual could bias an actor's reputation by putting more weight to acts of defection (not helping) than acts of co-operation (helping) or vice versa. We term this difference "judgement bias", and build an individual-based model of image scoring to investigate the conditions under which it may evolve. We find that, if the benefits of co-operation are small, judgement bias is weighted towards acts perceived to be bad, while if the benefits are high, the reverse is true. Our results are consistent under both scoring and standing strategies. Allowing judgement bias to evolve has the further effect of favouring indirect reciprocity, and thus promoting the overall level of cooperation.

## **Inbreeding depression in female reproductive success in a small and isolated Swiss village**

*Erik Postma, Luigi Martini and Pietro Martini*

Despite overwhelming evidence for a negative effect of inbreeding in plants and non-human animals, its effect in humans remains subject to debate. In fact it was Darwin (who married his cousin and feared that the poor health and early death of several of his ten children was the result of "a serious form of inheritance from my poor constitution") who "wished that the truth of the often repeated assertion that consanguineous marriages lead to deafness and dumbness, blindness, etc., should be ascertained". His request for a large-scale investigation was turned down, and even today good evidence for negative fitness effects of inbreeding in humans remains remarkably scarce. In an attempt to obtain a better understanding of the effects of inbreeding in humans, we reconstructed the genealogies of the inhabitants of Cavergno, a small and isolated Swiss village, resulting in a unique data set consisting of over a thousand individuals, with records going back as far as the 17th century. We subsequently estimated the relatedness of all married couples, as well as the level of inbreeding for each individual. Accounting for temporal trends in both the mean inbreeding level and family size, we found no effect of parental relatedness on reproductive success, and no effect of inbreeding on lifespan. Importantly however, there was a significantly negative effect of the inbreeding level of the mother, but not of the father, on the number of offspring. So although related couples do not have fewer children, they will have fewer grandchildren, resulting in strong selection for inbreeding avoidance, also in humans.

## **Bayesian phylogenetics and the stochastic modeling of evolution**

*Fredrik Ronquist, Swedish Museum of Natural History, PO Box 50007, SE-104 05 Stockholm, Sweden; fredrik.ronquist@nrm.se*

Over the last few decades, phylogenetics – the inference of evolutionary trees – has become an essential analytical tool across the life sciences. For a long time, phylogenetics was dominated by very simple methods due to the computational complexity of standard statistical approaches. The original maximum likelihood algorithms relied on slow optimization of nuisance parameters, leading to the development of iterative approaches and reluctance to explore other than the simplest of models. The introduction of Bayesian MCMC techniques about ten years ago changed all of this. The capability of the MCMC approach to efficiently handle more complex and realistic evolutionary models has led to a virtual explosion in model development to the benefit of evolutionary biology as a whole. I review some of the more exciting recent developments in stochastic models of evolution, including the modeling of morphological evolution, the relaxation of the molecular clock, accommodation of process heterogeneity across sites and lineages, and incorporation of insertions and deletions in models of sequence evolution.

## **Look who's watching: cleaner fish *Labroides dimidiatus* adjust audience effects to the quality of bystanders**

*Ana Pinto, Ralph Bergmüller & Redouan Bshary*

Cleaner fish *Labroides dimidiatus* increase service quality to current clients in response to image-scoring clients. The advantage of such amendments is that cleaners gain access to the observers. Are these audience effects fixed behavioural patterns or do cleaners fine-tune their behaviour? If they do, they should increase service quality in particular if the bystander is an attractive food source relative to the current client. To test this idea on 21 cleaners two Plexiglas plates of different size with differing amounts of food on them were presented to cleaners either alone or in the presence of the other plate. Plates contained preferred prawn items (mimicking client mucus) and less preferred flake items (mimicking client ectoparasites) and were removed immediately in response to cleaners eating prawn. In the two-plate situation, cleaners could gain access to the “observing” plate by eating only the less preferred food off the accessible plate. I found that cleaners feed more against their preference if they thereby gain access to a large additional food source but not if they would gain access to a small additional food source. In a second experiment, I found that cleaners are even capable of refraining completely from feeding on the first Plexiglas plate, producing fake bites or tactile stimulation with their fins instead. The results show that cleaners are remarkably fine-tuned in their foraging decisions and hence levels of cooperation.

## **Transcriptional basis associated with queen acceptance and execution in *Solenopsis invicta***

*Mingkwan Nipitwattanaphon, John Wang, Laurent Keller*

Very few natural polymorphisms affecting behavior have been identified. In fire ants, a single mendelian locus, Gp-9, is fully associated with a social form polymorphism. Colonies are either monogynous, containing only a single queen who are always of the Gp-9 BB genotype, or polygynous, containing many queens who are always Gp-9 Bb. The difference in queen genotypes in the two social forms is maintained, in part, because workers recognize an odor difference between the two queen genotypes. Queen recognition by workers could potentially be mediated by Gp-9 as it encodes a putative odorant binding protein. However, the genes involved in generating the odor differences and other physiological and behavioral differences in queens are unknown. In an attempt to find such genes, we used cDNA microarrays to profile gene expression of mature virgin queens. We found approximately 30% of the genes on our microarray (~3,500 out of 11,864) are differentially expressed between the Gp-9 BB and Bb genotypes. These genes include many encoding odorant binding proteins (OBPs) and chemosensory proteins, as well as regulatory proteins, reproductive proteins, and transposons. We compared our data to previous microarray data from workers. Interestingly, this comparison suggests an additional candidate gene encoding an OBP that may function in workers for queen recognition. Details of our results and analysis will be presented.

## **Reliability of the detection of loci under selection using genome scans**

*Samuel Neuenschwander, Frédéric Hospital, Jérôme Goudet*

A central focus of evolutionary biology is to map the genetic basis of natural selection. Natural selection shapes the genetic variation within and between loci. The so-called genome-scan approach takes advantage of it trying to detect regions of the genome with unusable high or low genetic variation. In order to detect such outlier values coalescent simulations are often used to generate an appropriate reference distribution. The aim of this study is to investigate how reliable such reference distributions are. Especially, we were interested if the genetic variability varies if loci are simulated independently or within the same genome and to address the effect of physical linkage on the genetic variability. Our results show that in general the genetic variability is robust to the method the genetic variability is generated. However, the different methods may vary significantly at the extremes of the distributions. And this is exactly the site of the reference distribution used to define outlier values. Consequently genome scans may lead to an excess of outliers, i.e. detection of outlier loci which are purely neutral.

## **Body size vs. phylogeny as determinants of food-web structure**

*Russell E. Naisbit; Patrik Kehrl; Louis-Félix Bersier*

Classical theory on food web structure has emphasized the key importance of body size to understand who eats whom in natural communities. More recently, phylogeny has been suggested as a more fundamental level of explanation. Here, we compare the relative importance of these two factors on food-web architecture. We first compute three similarity matrices for the species comprising each of 12 highly resolved webs, based on trophic, body size, and taxonomic information (these matrices capture the community structure based on each of the three descriptors used). We test the relationship between these similarity matrices with simple and partial Mantel tests, which allows us to perform a path analysis. We find that both body size and phylogeny are significantly linked to trophic structure. However, for the vast majority of webs, phylogeny is of primary importance. This highlights the need to include macro-evolutionary patterns in ecological models of community structure.

## **Two to Tango, Three to Rock**

*Suter S. M., Keiser M. & Meyer D.R.*

For diploid organisms with sexual reproduction, propagating their own alleles means also propagating the alleles of someone genetically unrelated, the mate. Mate choice, intrasexual and sperm competition are the behavioral instruments of birds to assure the right alleles to their progeny. Because of extra-pair (EP) copulations, mate choice in passerine birds may take place more than once in a breeding season even when the social partner remains the same. The criteria for choice may be different each time. We used our 6-year paternity data on a free living Reed bunting population to test ideas on mating systems. The choice of a social partner was related to arrival dates. Successful EP males were often paired, nearest neighbor males. Male EP reproductive success was correlated with age and dawn song rate/ song diversity. The feeding rates of males correlated negatively with the number of EP young in their nest. Since EP young were genetically more heterozygous than intra-pair young and since the successful EP males were genetically more dissimilar to females than the non-successful ones we speculate that, sperm selection took place. The EP fledglings have been shown to have a higher survival rate after leaving the nest than intra-pair young. There is therefore a genetic benefit in having EP young for both the fathers and the mothers. We estimated that the costs for both males and females of EP behavior were lower than the benefits. We conclude that, if it takes two to Tango, it takes three to Rock.

## **Egg discrimination by workers in the ant *Formica selysi***

*Joël Meunier, Luma Delaplace, Michel Chapuisat*

The maintenance of sociality despite potential conflicts requires robust regulatory mechanisms. Eusocial colonies are characterized by reproductive division of labour, with non-fertile helpers raising the brood of other individuals. In social Hymenoptera, workers may be able to discriminate eggs laid by nestmate workers, nestmate queens, or foreign queens when such discrimination increases their inclusive fitness. In this study, we tested whether workers from either single-queen or multiple-queen colonies of *Formica selysi* discriminated eggs according to their origin. Specifically, we set up groups of workers in which we introduced nestmate worker-laid eggs, nestmate queen-laid eggs or foreign queen-laid eggs and recorded the speed at which eggs were collected by workers, as well as the survival of eggs. Workers from single- and multiple-queen colonies discriminated worker-laid from queen-laid eggs, which suggests that workers collectively police each other in both types of colonies. However, the elimination of worker-laid eggs seemed weaker in single-queen colonies, possibly because workers self-restrain from reproducing in these colonies. Workers from single-queen colonies discriminated against eggs laid by foreign queens, as compared to eggs laid by nestmate queens, whereas workers from multiple-queen colonies did not make this distinction. Such reduced discrimination in multiple-queen colonies may maintain a veil of ignorance about the maternal origin of queen-laid eggs in order to avoid costly intracolony conflict due to nepotism. Overall, workers exhibit a remarkable ability to discriminate eggs, which seems finely tuned to colony queen number in order to prevent selfish individuals from exploiting the group resources.

## **Temporal organisation in an ant colony**

*Danielle Mersch, Alessandro Crespi, Laurent Keller*

The success of organisms and social groups depends largely on their aptitude to synchronize activity and rest with the optimal period of the day, thereby generating a circadian rhythm. This rhythm has been shown to be intimately associated to natural cycles. However, because it has been difficult to monitor simultaneously all individuals in a social group, the influence of the social environment on the activity rhythms remains largely unstudied. Here, we study the social influences on the temporal organisation of activity in an ant by filming entire colonies of labelled individuals continuously under 12 hours light – 12 hours dark cycles and under constant darkness. We show that workers greatly vary in their rhythmic pattern, some individuals presenting a 24-hour rhythmicity while others show shorter or longer rhythms or even appear arrhythmic. At the colony level, a rhythmic pattern emerges from the grouped individual rhythms, which suggests that the temporal organisation of a colony differs considerably of that of its constitutive members. These findings underline the importance of considering the social environment when studying activity rhythms.

## **Globally invading plant pathogens: Rapid evolution via episodic selection and interspecific gene transfer.**

*Clive Brasier, Forest Research, Farnham, Surrey GU10 4LH, UK*

Episodic selection – a major shift in one or more routine components of selection – can lead to accelerated microevolution in fungi. Invasion, an extreme episodic selection event, can provide the additional opportunity of rapid evolution through gene transfer between invasive and resident species. Sympatric fungi generally exhibit strong barriers to inter-specific gene flow and, until recently, fungal hybrids were considered rare. Allopatric fungi - arising in geographic isolation - may not have evolved such barriers. Today, many previously geographically isolated fungi are being brought into contact by man, and there appears to be an associated upsurge in fungal hybridisation events, notably among fungal plant pathogens. Some events are of considerable environmental significance. Examples include *Phytophthora alni*, an allopolyploid hybrid swarm probably recently evolved in a European nursery, now killing alders across Europe; and hybrids between European and American species of *Heterobasidion*, a serious pine root pathogen, now establishing on the Italian coast.

I will discuss the case of the anciently divergent Dutch elm disease pathogens and *Ophiostoma ulmi* and *Ophiostoma novo-ulmi*, responsible for killing billions of mature elms in the first and current pandemics of

Dutch elm disease respectively. *O. novo-ulmi* has recently spread across the northern hemisphere. In doing so it has acquired 'useful' regulatory genes - vegetative compatibility and mating type genes - from the resident *O. ulmi* via interspecific gene transfer; and discarded *O. ulmi* DNA (e.g. pathogenicity and toxin genes) exerting a negative effect on fitness. This appears to have enabled *O. novo-ulmi* to survive the spread of deleterious viruses in its migratory populations. The same viruses might otherwise have prevented the current pandemic. This phenomenon has considerable implications for the adaptation of invasive fungi to new or disturbed environments. It may also be the first example of interspecific transfer of regulatory genes in a eukaryote.

### **Differential male mating success according to genetic compatibility**

*Lindholm, Anna & Koenig, Barbara*

If mate choice for genetic compatibility occurs, it should be most easily seen in systems where the cost of incompatibility is high. In house mice, a driving selfish genetic element in house mice, the t-haplotype, causes zygote inviability when homozygous. Our data from lab crosses show that when a male heterozygous for the t-haplotype sires the offspring of a heterozygous female, half of her offspring die before birth. Half of the offspring die, rather than the expected quarter, because meiotic drive in t-bearing males leads to nearly all of his offspring inheriting his t-haplotype. In order to avoid the cost of this genetically incompatible mating, heterozygous females should preferentially mate with wildtype males. We analysed paternity using molecular genetic methods in a wild population of house mice in Switzerland in which half of adult males are heterozygous for the t-haplotype. If paternity reflects mating patterns, then heterozygous females were significantly more likely to mate with wildtype than with heterozygous males. Alternatively, paternity might reflect post-copulatory mate choice or sperm competition. In either case, our evidence provides rare support for differential male mating success according to the potential for intragenomic conflict.

### **Sex-specific benefits in the *Silene latifolia* – *Hadena bicurris* nursery pollination system: male moths as mutualism rescuers**

*Anne-Marie Labouche and Giorgina Bernasconi*

Conflicts of interest underlie mutualisms, including nursery pollination, in which the pollinators lay eggs inside the flowers and offspring consume the developing seeds. Low benefits to costs ratio could destabilize such associations towards parasitism or even extinction. Pollination by males of the pollinator/seed predator may increase the net benefits and thus the stability of the interaction. We investigated the dioecious plant *Silene latifolia* (Caryophyllaceae) and its nursery pollinator, *Hadena bicurris* (Noctuidae). Data on visitation, behaviour and pollination efficiency in experimental plant patches demonstrate that (i) male moths are equally or even more efficient pollinators than females, and (ii) female and male moths do not preferentially visit one plant sex, which would impair pollen transfer. Male and female moths were equally likely to visit male and female flowers, fertilizing on average 45% of the ovules in one visit. Feeding behaviour was sufficient to ensure pollen transfer. The proportion of ovules fertilized per visit was not significantly affected by ovi-position behaviour. Male moths fertilized on average 1060 and females 1510 ovules per observation period. However, assuming that half of the primarily infested flowers will not produce any seeds, leads to a net estimate of only 945 fe-male-fertilized seeds. This indicates that male moths contribute to seed production, increasing the net benefits of the interaction. Accounting for the potential role of male insects as well as extending current models to dioecious plants with sexually dimorphic strategies might provide novel insights into the factors that contribute to stabilize mutualistic interactions.

## **Fast early growth impairs later cognitive performance in a cichlid fish**

*Alexander Kotrschal, Barbara Taborsky*

After a period during which growth is depressed through poor nutrition many organisms show compensatory growth after normal food levels have been restored. Growth compensation allows organisms to mitigate the effects of prior growth depression, and organisms can reach similar sizes as, or even outgrow individuals, which never experienced periods of poor nutrition. This shows that, instead of growing at maximal speed under optimal nutritional conditions, organisms rather grow at optimal rates, indicating that costs arise from growing too fast. Costs shown to be associated with fast growth range from reduced overall growth rate, impaired starvation resistance, delayed age at sexual maturation, higher risk of adult obesity and a reduced lifespan to decreased locomotor performance, increased predation risk and impaired cognitive performance. Investigating the link between cognitive abilities and growth trajectories we individually raised 140 cichlid fish (*Simochromis pleurospilus*) under different experimental feeding regimes and determined their growth rates repeatedly at different stages during ontogeny. We tested whether juvenile and adult performance in a conditioning task was linked to variation in early growth trajectories of the fish. Early growth rates were tightly linked to juvenile cognitive performance. Surprisingly, we found that fast early growth impairs adult cognitive performance only when it occurs in a specific, very short time period of the juvenile phase. To our knowledge this is the first study showing that fast juvenile growth seems to impair brain development only during a certain critical time window. This result allows to generate predictions about the respective brain regions most actively developing during the identified critical windows.

## **The genetic and eco-morphological diversity underlying parallel evolution in the Tropheini, a group of cichlid fishes from Lake Tanganyika, East Africa**

*Adrian Indermaur & Walter Salzburger*

The species flocks of cichlid fishes in East Africa provide an excellent system to study explosive speciation and parallel evolution. More than 1500 species of cichlids have emerged in the East African Great Lakes in independent adaptive radiations. These radiations are characterized by rapid and non-bifurcating cladogenesis, so that the resulting species exhibit more or less equal genetic distances to one another. Due to the close relatedness of the species, the evolution of eco-morphological traits must have occurred on similar genetic backgrounds. Here we evaluate how, in cichlids, within and between-species genetic diversity is interrelated with ecological and morphological diversity. To this end, we inferred the phylogenetic and population genetic structure of several species of the Tropheini, a tribe of mostly rock-dwelling cichlids from Lake Tanganyika, on the basis of a mitochondrial locus and four nuclear genes. As proxies for ecological and trophic diversity, we measured N15 and C14 stable isotope ratios and performed geometric morphometric analyses based on body shape and the morphology of the lower pharyngeal jaws. The comparison of molecular phylogenies with morphological traits indicates a high level of parallel evolution of trophic specializations within the Tropheini. Our analyses show that eco-morphological diversity cannot be explained by either within-species genetic diversity or genetic relatedness.

## **Phylogenetic History and Population Structure of a large post-glacial adaptive radiation: the Alpine Lake Whitefish**

*Hudson, A. G., Vonlanthen, P., & O. Seehausen*

Recent taxon radiations are model systems for investigating the mechanisms of speciation and adaptive radiation and ultimately the origin and maintenance of biodiversity. Phylogenies remain key to establishing the relationships of taxa within a radiation and thus act as the bedrock on which different hypotheses may be tested. However as recent radiations are characterized by weakly differentiated taxa, with limited time for lineage sorting between speciation events and often incomplete reproductive isolation, phylogenetic studies with low numbers of independent genetic loci have struggled with limited resolution and discordance between datasets. The Central European lake whitefish (*Coregonus lavaretus*) complex are a classic example of a recent radiation, colonizing the Swiss Lakes following the retreat of the glacial

ice (<15,000 BP). Subsequent to this they have radiated into a unique array of endemic lake flocks, each with 1 to 6 described sympatric species differing in morphology and feeding and spawning ecology. Here we present a genomic investigation into the relationships between the constituent taxa of the Central European lake whitefish. Comparing the signal between 1328 AFLP loci and 1178 bp of non-recombining mitochondrial control region we reconstruct the phylogeographic and phylogenetic origins of this group and test hypotheses on the geography of speciation. We also utilise population genetics methodology for a more indepth study of population structuring amongst the described taxa within the lake flocks.

### **Geographic variation in life-history traits of the moor frog (*Rana arvalis*): environmental acidity drives adaptive divergence in metamorphic size and age**

*Sandra Hangartner, Anssi Laurila & Katja Räsänen*

Natural populations often inhabit spatially heterogeneous habitats, which results in divergent natural selection. Theory predicts that the extent of phenotypic divergence among populations should correlate positively with the strength of divergent selection. In slow growth environments with seasonal time constraints, such as acid environments in northern latitudes, selection should counteract negative effects on growth and developmental rates. In amphibians, metamorphic size and age are important fitness components and among population variation in breeding pond acidity should therefore cause divergent selection on larval growth and development rates. The aim of this study was to test the predictions that i) environmental acidity drives divergence in larval life-history traits (viz. metamorphic size and age) and ii) that the extent of phenotypic divergence is correlated with differences in breeding pond pH (i.e. the strength of divergent selection). We tested these predictions on eight Swedish moor frog populations, inhabiting a pH gradient from pH 4.2 to 7.4, in a common garden experiment. We conducted artificial crosses and reared larvae from hatching to metamorphosis in the laboratory in two pH treatments (pH 4.3 and 7.5). Our main results show that metamorphic size and age are negatively correlated with breeding pond pH (stronger divergence for larger differences in pH). This indicates that acidity selects for faster growth but slower developmental rates, and supports the prediction that the strength of divergent selection on larval life-history traits varies with environmental pH in the moor frog.

### **Dominance and cis-regulatory gene expression.**

*Pierre Fontanillas, Bernardo Lemos, Luciana O. Araripe and Daniel L. Hartl*

The genetic architecture underlying abundant gene expression diversity within and between populations remains elusive. We investigated the role of dominance in the segregation of cis- and trans-regulation within and between populations. We used chromosome substitution lines of *Drosophila melanogaster* to show that (i) >70% of the genes that are differentially expressed between two homozygous lines are masked in the heterozygous, suggesting that one of the substituted chromosomes contains a recessive allele; (ii) such large masking is already obtained with heterozygous chromosomes originating from the same population, with the time of divergence between chromosomes in heterozygous lines making only a small but significant contribution to the masking of variation observed in homozygous lines; (iii) variation in gene expression due to trans-regulation is biased toward greater deviations from additivity because of recessive and dominant alleles, whereas variation due to cis-regulation shows higher additivity; and (iv) genetic divergence between second chromosomes is associated with increased cis-regulation, whereas the level of trans-regulation shows little increase over the time scale studied. Our results indicate that cis-acting alleles may be preferentially fixed by positive natural selection because of their higher additivity, and that the disruption of gene expression by recessive variation with pervasive trans-effects may be important for understanding gene expression variation within populations.

## **Selfish genetic elements and sexual selection**

*Nina Weddell, University of Exeter UK*

Selfish Genetic Elements (SGEs) are genes, organelles or microorganisms present within the genome or cell of an organism that employ various tactics to increase their transmission rate relative to the rest of the host genome to the next generation. SGEs are ubiquitous in all living organisms and are often associated with fitness cost to the bearer. 'Sex Ratio' (SR) drive in *Drosophila pseudoobscura* result in female only broods due to elimination of Y-bearing sperm during meiosis. However, SR males are poor sperm competitors and, as a consequence, polyandrous females sire a higher proportion of males. Polyandry also reduces the risk of population extinction due to lack of males, as it decreases the frequency of SR. In addition, females in population with SR evolve increased remating rates, as predicted if polyandry is a strategy to reduce the risk of siring offspring carrying SGEs. These results illustrate the intimate interactions between a SGE (SR drive) and female mating behaviour. It is possible SGEs in general favour polyandry and sperm competition to reduce the risk to females of fertilizing their eggs with sperm from SGE-carrying males with reduced fertility.

## **Future distributions of mountain plants under climate change: does dispersal capacity matter ?**

*Robin Engler, Christophe Randin, Pascal Vittoz and Antoine Guisan*

Assessing the potential impact of predicted global climate change on vegetation is a pressing matter. While a number of studies have already forecasted the possible impact of climate change on plant distributions using models based on ecological niche theory, most of them have ignored dispersal-limitations. Instead, they assumed dispersal to be either unlimited or null. However, depending on the rate of climatic change, the landscape fragmentation and the dispersal capabilities of individual species, these assumptions are likely to prove inaccurate, leading to under- or overestimation of future species distributions, and potentially yielding large uncertainty between these two extremes. To quantify the importance of taking dispersal limitations into account, we developed a cellular automaton able to simulate plant dispersal under climate change, and carried-out projections of future distribution over the 21st century for 287 mountain plant species in a study area of the Western Swiss Alps. For each species, we compared results obtained from simulations accounting for realistic dispersal with those obtained from unlimited and no-dispersal simplifications. Although simulations accounting for realistic dispersal limitations did significantly differ from those considering dispersal as unlimited or null in terms of projected future distribution, using the unlimited dispersal simplification nevertheless provided good approximations for species extinctions under more moderate climate change scenarios. Overall, simulations accounting for dispersal limitations produced, for our mountainous study area, results that were closer to unlimited dispersal than to no dispersal. Finally, analyzing the temporal pattern of species extinctions over the entire 21st century showed that, due to the possibility of a large number of species shifting their distribution to higher elevation, important species extinctions for our study area might not occur before the 2080-2100 time periods.

## **Effect of genetic exchange on plant gene expression**

*Colard Alexandre, Sanders Ian*

Arbuscular mycorrhizal fungi (AMF) are obligate symbiotic fungi associated with the majority of terrestrial plant species. They improve plant nutrition and promote their diversity and in exchange, plant supplied carbon to the fungi. Although AMF were thought to be ancient asexuals, we have recently been able to make crosses between "parental" isolates and test the influence of mixed genotypes on phenotypic and genetic traits. The crossed isolates are heterokaryotes and exhibit a variable bi-parental inheritance. Interestingly, this variability in nuclear composition of the cytoplasm may have a great influence on phenotypic traits of the associated plants, such as their growth, but its influence on gene expression remained poorly known. A recent study on *Oriza sativa* found 18 genes exclusively expressed in presence of AMF, suggesting specific interactions between genomes of AMF and host plants. Here, we used real-time PCR to test the expression of 12 of these genes on the host *Oriza sativa*. Specifically, we investigated potential variation in gene expression of parental and crossed isolates of AMF at 6, 9 and 12

weeks. We found that gene expression was significantly influenced by the type of isolate colonized. Four genes are differently expressed between isolates at different time, and three of them show a difference between crosses and parents, suggesting an effect of mixed fungi genotype on plant genotype. These results showed the amazing potential effect of the AMF on plants and open new perspectives for the agriculture.

### **Birth and death in the avian MHC**

*Reto Burri*

To date, the evolutionary history of the major histocompatibility complex (MHC) in birds remains obscure. The high rates of concerted evolution found in this lineage, together with frequent gene duplication and gene loss inherent to MHC evolution blurred the footprints of gene history. Only recently, first insights into the phylogenetic relationships of MHC genes among avian orders were brought to light, suggesting either the presence of 2 ancient avian MHC lineages, or convergent evolution. Based on phylogenetic analysis of silent site variation, we now show that the 2 major avian MHC lineages are the likely result of a single gene duplication preceding the major avian radiation. Subsequent to duplication, the ancient avian MHC lineage evolved in a conserved fashion, while positive selection was driving the divergent evolution of the newly arisen lineage. Along with the evolution of modern bird orders, each MHC lineage was lost at least once. This is the first demonstration that, as in mammals, MHC evolution in birds over the long run is driven by processes of birth and death, and divergent selection.

### **Public good in fishes**

*Andrea Bshary*

Reef fishes frequently get bitten by parasitic sabre tooth blennies (*Plagiotremus rhinorhynchus*, *P. tapeinosoma*). After being bitten by the parasite victims can react with flight or aggressive behaviour. Experiments with Plexiglas plates in the lab showed that aggressive behaviour towards blennies serves as punishment (Blennies learn to avoid punishing individuals). Observations in the reef showed that aggression towards blennies creates a public good: if the blenny gets aggressed by a victim after taking a bite, it is more likely to choose its next victim from another species than after the victim reacted with flight behaviour. This means that all members of a big shoal of look-alikes profit from individual aggressive behaviour. I will discuss why this does not lead to a social dilemma and why therefore the punishing behaviour does not cease in big shoals of fishes.

### **Genetic analysis of reproductive strategies in the primitively eusocial halictid bee *Halictus scabiosae***

*Nayuta Brand, Michel Chapuisat*

The evolutionary origin of cooperation is one of the major enduring questions in biology. Social halictid bees are good model systems to investigate the factors promoting sociality, because part of the female offspring remains in their nest to act as workers even if all females would have the capacity to mate and lay eggs. We investigated the genetic relatedness and pedigree structure within nests of the halictid bee species *Halictus scabiosae*. This species has an annual colony cycle and produces two consecutive broods. The first brood consists normally only of females that act as workers, while the second brood develops into reproductive individuals. We tested whether the first and second brood females were produced by the same queen and reconstructed the sibships within the nests with the help of 11 microsatellite loci. The average relatedness between first and second brood females within the same nests ( $r = 0.59$ , 95% CI = 0.55 to 0.63) was significantly lower than the expected value for full sisters ( $r = 0.75$ ), whereas the relatedness among the first ( $r = 0.73$ , 95% CI = 0.67 to 0.79) and second ( $r = 0.72$ , 95% CI = 0.68 to 0.77) brood were consistent with offspring being full sisters. In the reconstructed sibships, we found indices that part of the second brood may be produced by first brood females. Overall, *H. scabiosae* has very flexible reproductive strategies and a status intermediate between solitary and highly social species, which calls for further studies on female options and fitness payoffs in this species.

## **Variable progress toward ecological speciation in parapatry: stickleback across eight lake-stream transitions**

*Daniel Berner, Andrew P. Hendry*

Divergent selection between contrasting habitats can sometimes drive adaptive divergence and the evolution of reproductive isolation in the face of initially-high gene flow. "Progress" along this ecological speciation pathway can range from minimal divergence to full speciation. We examine this variation for threespine stickleback fish that evolved independently across eight lake-stream habitat transitions. By quantifying stickleback diets, we show that lake-stream transitions usually coincide with limnetic-benthic ecotones. By measuring genetically-based phenotypes, we show that these ecotones often generate adaptive divergence in foraging morphology. By analyzing neutral genetic markers (microsatellites), we show that shifts in resource use and morphology across the ecotones are often associated with the presence of two populations maintaining at least partial reproductive isolation in parapatry. Coalescent-based simulations further suggest that these populations may have diverged in the face of gene flow within a few thousand generations. Despite these generalizations, we also find striking variation among the eight lake-stream transitions in progress toward ecological speciation. This variation allows us to hypothesize that progress is generally promoted by strong divergent selection and limited dispersal across the habitat transitions. Our study thus makes a case for ecological speciation in a parapatric context, while also highlighting variation in its outcome.

## **Maintenance of genetic polymorphism in a host-parasite system: an experimental evolution approach**

*Berenos C, Wegner KM, Schmid-Hempel P*

In a landmark paper, Haldane (1949) proposed that selection by pathogens is the major factor maintaining the substantial amount of genetic variation that is found in natural populations. Theoretical "Red Queen"-type models now show that antagonistic host-parasite co-evolution might indeed maintain a host genetic diversity by time-lagged negative-frequency dependent selection, and at the same time select for increased host recombination rates. To test Haldane's postulation, and we used an experimental evolution approach simulating an arms race between the host *Tribolium castaneum* and its natural microsporidian parasite, *Nosema whitei*. In detail, we created 8 host lines which were subjected to a full factorial design including population size (small (n=50) vs. large (n=500)) host and control vs. co-evolution with *N. whitei* for a total of 8 discrete generations. 11 neutral molecular markers distributed over 5 linkage groups were used to infer the dynamics of heterozygosity and linkage disequilibrium. We found that drift is a strong force, strongly reducing genetic variation in small populations. Selection by parasites counteracted drift as parasitized populations have significantly higher levels of heterozygosity and was especially strong in large populations. Together with the underlying complex genetic architecture of resistance against parasites, such selective maintenance of genetic diversity will also have implications for the evolution of recombination.