Mathematical Models in Ecology and Evolution 2009

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— Abstracts —

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Preface

The first Mathematical Models in Evolution and Ecology meeting was organised by Mark Broom in 2007, at the University of Sussex. Such was its success that there was great interest in establishing it as a regular meeting series, and we are pleased to host the second MMEE at the University of Bristol. With MMEE 2009 we are marking the bicentennial of Darwin's birth, and 150 years since the publication of On the Origin of Species. Biology and evolutionary theory have moved on a long way since Darwin's times, both in the depth of our understanding and in the techniques available to us. Mathematical modelling is now fundamental to both fields. Darwin formulated his theory without knowledge of how traits are inherited – he assumed that inheritance occurred by a blending of parents' characteristics, despite Gregor Mendel publishing evidence for the discrete, genetic nature of inheritance only six years after publication of The Origin of Species. When Mendel's results were rediscovered and interpreted by the scientific community, it took mathematical modellers such as R.A. Fisher, Sewall Wright and J. B. S. Haldane, working in the first half of the twentieth century, to reconcile genetics and evolutionary theory in what is now known as the 'synthetic view of evolution', or 'modern synthesis'. Darwin himself was no mathematician, arriving at his startling conclusions solely through observation of the natural world and verbal reasoning. However, his ideas find natural expression as mathematical models of how gene frequencies change in populations over time, and Darwin's theory was vindicated and strengthened by these earliest modelling efforts.

Even after so much time has passed, Darwin's ideas remain as current and exciting as they did on first being revealed to the world. Many of the mathematical frameworks developed by Fisher, Wright and Haldane are also still in widespread use today. What has changed is that many of today's biologists are often much more comfortable than Darwin was with presenting purely theoretical results, so that they or others might subsequently look for confirmatory evidence. For those working in the field of theoretical biology, Darwin's work still represents a treasure trove of ideas to be modelled, investigated and refined. Mathematical models are now used extensively to address the problems that Darwin himself was concerned with. The keynote speakers of MMEE 2009 reflect this, covering the state-of-the-art in modelling speciation (Franjo Weissing, Groningen), the evolution of sex and sexual selection (Hanna Kokko, Helsinki) and the evolution of social behaviour (Rob Boyd, UCLA), and giving also a direct link to and historical perspective on the 'modern synthesis' (A.W.F. Edwards, Cambridge). In addition to this, of course, we have a full programme of 80 oral presentations and 12 posters on various aspects of modelling in ecology and evolution. We hope that you find the conference as stimulating to attend as we have found it to organise.

James A.R. Marshall, John M. McNamara, Alasdair I. Houston
Bristol, 7th August 2009

Abstracts

Mutant fixation, diversification and speciation in a dynamic landscape

R. Aguilée, D. Claessen and A. Lambert

The evolution of subdivided populations is often analyzed using metapopulation models in which the landscape - defined as number, size and connectivity of subpopulations - is static in time. Yet natural populations are often subjected to repetitive fragmentation and secondary contact due to geological, climatic or ecological processes. Such landscape dynamics, which may occur at different spatiotemporal scales, influence drift, selection, and speciation. Here we study the short and long term evolution of a population in such a dynamic landscape. First, assuming that a population is alternatively panmictic or split into two demes, we examine mutant fixation. Using diffusion approximations, coalescent population effective sizes, and simulations, we show that: (i) the landscape dynamics can generate repetitive founder effects which counteract selection; (ii) depending on the characteristic timescales of the landscape dynamics, a refuge effect can strongly delay mutant fixation. Second, we study long term evolution and speciation under the same landscape dynamics. Using adaptive dynamics, we analyze the case where resources are unevenly distributed over the landscape. The landscape dynamics then allow for allopatric speciation with local adaptation during the allopatric phase, while the sub-populations are forced into secondary contact during the sympatric phase. We study the long term evolution of this system in case the sympatric phase is characterised as a either continuously stable strategy or an evolutionary branching point.

Logistic populations in a patchy environment

V. Alonso, T.J. Sluckin and C.P. Doncaster

Fagan *et al.* [1] have discussed biogeographical issues using a generalised logistic model. Here we examine a related mathematical model of a population in an inhomogeneous environment. The model consists of a disordered aggregate of good and bad patches. In good patches, the population obeys logistic growth plus diffusion. In bad patches, diffusing populations are unable to sustain themselves. We compute effective logistic properties for the whole system. Specific properties of interest include the intrinsic per capita rate of growth of the population, the diffusion constant and the carrying capacity per unit area. Calculations are made both in one and two dimensions. In one dimension we find that the presence of a low density of large bad regions may significantly influence the effective diffusivity. This should be borne in mind when applying mathematically tractable toy one-dimensional models to real species of conservation concern. In two dimensions, the most important factor for the effective diffusion constant is whether the good or the bad regions are topologically connected. Diffusion is reduced not only by lack of diffusion per se, but also by high mortality in bad regions. We give semi-analytic formulae for the key effective quantities for the limits of circular good patches in a topologically connected sea of bad patches, and vice versa. Finally we discuss our results in the context of the development of efficient strategies for maintaining biodiversity and/or pest-elimination.

[1] W.F. Fagan, R.S. Cantrell, C. Cosner and S. Ramakrishnan, Am. Nat. 173, 363-375 (2009)

A formal model of mutual mate choice with age dependent preferences

S. Alpern, I. Katrantzi and D. Ramsey

We develop a formal game theoretic model of mutual mate choice in which males and females have an integer age, which increases in every period. Given numbers of unmated males and females of age 1 (first year of fertility) enter in each period. In each period unmated males and females are randomly paired and form a couple if they both accept each other. The utility of a couple is their number of mutually fertile remaining periods, with males fertile up to age m and females up to age n. We establish some general theoretical results and determine the equilibrium acceptance strategies for various values of the parameters, including the incoming sex ratio. Equilibria are steady state and subgame perfect. In some cases there are no pure strategy equilibria, but in these cases there are mixed equilibria. We then introduce and solve a continuous time analog, which represents a limiting case in which the number of periods goes to infinity but the meeting probability in each period goes to zero. In both versions our model predicts the age distribution of unmated males and females, and also the distribution of 'age at marriage'.

Dynamic multipopulation and density dependent large games: An alternative approach to modeling of evolution

K. Argasinski

Current approach to evolutionary game theory is mostly related to two-person matrix games. In biological applications there is a different interpretation of mathematical structure, but mathematical notions such payoff function or set of strategies are strictly the same as in classical economic game theory. Classical approach to evolutionary game theory is focused on elementary actions (pure strategies), instead of individuals. That is why classical evolutionary game theory is not compatible with individual based modeling. This fact leads to few interpretational problems, which will be presented in the talk. The solution of this problem is a new approach called 'dynamic multipopulation and density dependent large game'. We will present a general framework which allows to model interactions among any number of subpopulations including density dependence. We prove that all modern approaches to evolutionary games, except classical bimatrix approaches are closely related. All evolutionary models can be reduced to a single population general model by a simple change of coordinates. It will be shown that classical bimatrix (and generalized n-matrix) approach is inconsistent with other approaches because it does not depend on proportions between competing populations. It will be also shown that background fitness cannot be used to model density dependence, because this approach is incompatible with classical demographic and life history models and it is against basic probabilistic intuitions. The new approach is free from disadvantages of two-person games, and more universal. This method will bring the evolutionary games nearer to individual based modeling, classical demography and life history models.

The dynamics of a sex ratio self-regulation

K. Argasinski

In a classical sex ratio game, grandoffspring number is treated as a fitness measure of a female. The theory predicts that it is more profitable to produce offspring of the less numerous sex. The new model based on dynamic evolutionary large games shows that the dynamics of this system are complex and double-phased. First, a rapid phase is associated to convergence to 'fast' equilibrium and convergence of the secondary sex ratio to the value of the primary sex ratio. During this phase predictions of the new model differ in several aspects from classical theory. Trajectory of the secondary sex ratio can surpass the 0.5 value, which is an equilibrium in classical theory. Also, strategies in which frequencies should increase from the classical point of view, may decrease. A second, slow phase is responsible for the convergence of the primary sex ratio (and in effect secondary sex ratio) to 0.5 value. During this phase asymptotic predictions of the new model are compatible with the suggestions of the classical theory. However, surprising is that perturbation of the state of only male subpopulation may destabilize the whole system. Also surprising is that the reproductive success of a gene depends on the current sex ratio in the subpopulation of its hosts, not on the value of the encoded individual strategy. This is a newly discovered evolutionary mechanism called 'double- level selection'. Individual strategies affect the value and dynamics of the sex ratio in the hosts subpopulation by a so called 'tug of war' mechanism.

The maintenance of incompatible alleles in a subdivided population

C. Bank and J. Hermisson

The Dobzhansky-Muller model is frequently used to explain the emergence of intrinsic incompatibilities in allopatric populations. However, it is unknown if such incompatibilities survive secondary gene flow and therefore facilitate the evolution of postzygotic isolation, if there is no pure allopatry. Here, we studied a deterministic migration-selection model with two biallelic loci. We analysed the continuous-time dynamics of an island population receiving migrants from a mainland population, aiming to study the effect of epistasis versus local adaptation on the maintenance of polymorphism on the island. For the haploid model, under either zero or free recombination, we derived explicit formulas for the maximal migration rate limiting the maintenance of polymorphism at one or two loci. The diploid model yielded similar results, although in general this was not analytically solvable. Interestingly, we found that polymorphism at both loci can only be maintained if there is both local adaptation and epistasis. Neither a neutral Dobzhansky-Muller incompatibility nor a locally adapted allele alone can build a sufficient barrier to prevent loss of polymorphism at least at one locus in the presence of gene flow. This supports empirical results that found local adaptations clustering with incompatibilities in recently diverged species.

Cooperation among non-relatives evolves by state-dependent generalized reciprocity

Z. Barta, J.M. McNamara, D.B. Huszár and M. Taborsky

For decades attempts to understand cooperation between unrelated individuals have generated substantial theoretical and empirical interest in the evolutionary mechanisms of reciprocal altruism. Currently a growing body of research recognizes the cognitive limitations of animals that can hinder direct and indirect reciprocity because the necessary memory capacity is mentally demanding and costly. The recently found mechanism of generalized reciprocity works without advanced cognitive abilities. Here we show that cooperation can evolve by generalized reciprocity under a wide range of conditions, if individuals base their decision to cooperate on a state variable updated by the outcome of the last interaction with an anonymous partner. We show that by this alternative, state-based mechanism, generalized reciprocity can emerge through small evolutionary steps even in large groups. As it requires neither specific knowledge about the partners nor repeated interactions with them, this mechanism may help to understand the evolution of complex social behaviour without advanced cognitive abilities.

Modeling the evolution of aging

A. Baudisch

Is senescence inevitable? The results of a simple life history model show that optimal resource allocation over an organism's life can lead to senescent as well as non-senescent patterns of mortality and fertility. The model is based on a single state variable - vitality - that determines an organism's mortality, fertility and growth patterns, and it is solved via dynamic programming. The model goes beyond classic theory of the evolution of senescence. This theory predicts that evolution should inevitably lead to mortality that increases and fertility that decreases from reproductive maturity onwards for any conceivable species.

Modelling approaches in studies of animal migration

S. Bauer and M. Klaassen

Migration is a wide-spread phenomenon in the animal kingdom, including many taxonomic groups and all modes of locomotion, in rivers and oceans, on land and through the skies. Besides curiosity-driven research there is an increasing need to advance our knowledge of migrants in relation to the spread of emerging diseases, the proliferation of invasive species, aeronautical safety, as well as the conservation of migrants. Climate and global changes, habitat destruction and fragmentation, are increasingly considered to endanger migrants because of habitat loss, increasing distances between suitable stopover sites or mismatches in timing between food sources at distant locations. Thus, understanding the causes, consequences, determinants and evolution of migration of animals is critical to which modelling migratory behaviour may importantly contribute. Here, we review animal-migration modelling studies ranging from simple analytical models via game-theoretic model to individual-based, dynamic-state variable models and models based on evolutionary methods. We analyse each study with regard to the approach used, the focal species/ taxonomic group and the problem addressed with the model. Furthermore, we classify the various approaches and unify their nomenclature but also compare them with regard to data requirements and appropriateness and success in answering the many questions with which these models are challenged. Therefore, we strive not only for providing a handsome, stimulating guide to animal-migration modelling but also identifying caveats in present modelling approaches and techniques as well as to indicate some opportunities for future avenues.

'Zero-intelligence' evolutionary models and human behaviour

A. Bentley and P. Ormerod

Alfred Marshall, who founded the Department of Economics at Cambridge in 1900, conjectured that the real inspiration for the study of human behaviour in a socio-economic context would come from biology and the principles of evolution rather than physics. Economics, of course, has essentially chosen to follow the latter and not the former. For social scientists, models of evolution raise a fundamental problem. By definition, in the process of biological evolution, agents cannot act with purpose and intent. Nor do they have the ability to learn and hence adapt their decisions on the basis of the outcomes of previous decisions, 'taken' either by themselves or by other agents. We might usefully speak of human agents postulated to behave in this way as having 'zero intelligence' (Farmer *et al.*, PNAS, 2004). Conventional models predicated on cost-benefit decision making - deriving from economics - ascribe considerable intelligence to agents in the decision making process, both in terms of the information they gather and the rules they use to process it. This is the case even in models, for example, in which agents have incomplete information (Akerlof, Quart. J. Econ. 1970). In this paper, we propose a much different, parsimonious behavioural model much closer to the ZI model implied by biological evolution. It is capable of accounting for a wide range of phenomena observed in social, economic and cultural contexts. The widely used Albert-Barabasi network model of preferential attachment is simply a special case of this much more general model. In addition, the model produces the continuous turnover observed empirically within those distributions.

Testing a sexual conflict mate guarding model in an androdioecious crustacean

C. Benvenuto and S.C. Weeks

Intersexual conflicts occur often during reproduction, but they are difficult to assess. We pursued a new approach to the study of intersexual conflicts, using mate guarding behaviour in androdioecious crustaceans. Precopulatory mate guarding, a male strategy to monopolize mates, generates a sexual conflict on the duration of pairing prior to fertilization: costs and benefits of increased guarding duration are often asymmetrical between the sexes. Androdioecy (coexistence of males and hermaphrodites) allows for a better insight into sexual conflict because hermaphrodites are capable of facultative self-fertilization. This ability decreases the benefit of mating with a male. Thus, costs and benefits differ between the sexes even more than in dioecious species. We performed manipulative experiments to test a sexual conflict mate guarding model (Jormalainen, 1998). We measured: differential costs to male and hermaphroditic *Eulimnadia texana* during mate guarding (hermaphrodites were less able to feed than males); the influence of size as a form of differential power between the sexes (the higher the male/hermaphrodite size ratio, the longer the guarding); the optimal guarding time for each sex (by inhibiting the response of the other sex) and compared these to the compromised guarding time. Hermaphrodites preferred shorter guarding times (long ones being costly to them) while males guarded longer (not to lose mating opportunities). In androdioecious species the strength of the conflict is magnified because of substantial differences in costs (higher for hermaphrodites than males) and benefits (higher for males than hermaphrodites), providing strong evidence in support of the sexual conflict mate guarding model.

When can variation in host tolerance to parasitism be maintained?

A. Best

To defend themselves against parasitism hosts can either invest in resistance, where the host 'fights' the parasite, or in tolerance, where the host 'learns to live with the consequences' of disease. Previous evolutionary theory suggests that variation in resistance can arise through evolutionary branching but that branching is not possible in tolerance. This is in contrast with experimental results that find considerable variation in tolerance. We make use of a result from the geometric form of adaptive dynamics, which highlights the role of the trade-off between defence and its costs, to investigate under which circumstances evolutionary branching can occur in host tolerance. We find that branching, and therefore variation, can arise when there are trade-offs both between the tolerance and resistance mechanisms with an overall cost to defence, and when tolerance is to the sterility effects of disease rather than the mortality effects.

Social evolution: Progress and problems

R. Boyd

Many species live in cooperative societies in which individuals seem to sacrifice in the interest of the whole. Darwin was acutely aware that such behavior was a challenge to his theory, but he never was able to explain how it could evolve. Over the last half century there has been immense progress in our understanding of how natural selection gives rise to cooperative social behavior. Partly this is the result of mathematical work which has clarified the importance of non-random interaction resulting from both population structure, cues about relatedness, and facultative behavior in response to past behavior. Interestingly, the result has been a powerful theory that makes sharp predictions about one shot interactions among kin, but a much weaker theory about repeated interactions that has little predictive power. In recent years, an interest in the evolution of complex, large scale human societies has led to work on the cultural evolution of cooperation. This theory is in a confused state, I will argue, because a number of authors have imported the wrong tools from biology.

Adaptation is prevented at species margins where population size is limited

J.R. Bridle, J. Polechova, M. Kawata and R.K. Butlin

All species are restricted in their distribution. These range limits are caused by the failure of populations to adapt to changing ecological optima. However, evolutionary models cannot explain this failure because, even for a very rapid change in optima in space, genetic variance increases due to dispersal across an ecological gradient. This genetic variance should allow adaptation to almost any steepness of ecological gradient. However, stochastic factors are missing from these models. We present results from a simulation that follows as closely as possible analytical models, and which for high population sizes matches very closely deterministic predictions. However, for lower population sizes, adaptation along steep selective gradients is prevented. However, a lack of genetic variance does not explain this departure from the predictions of analytical models. Instead, demographic stochasticity in finite populations limits the ability of a population to adapt to the changing gradient and expand to available habitat. In addition, populations also fail to track the changing optimum at high values of dispersal. This seems to be due to constraints on the evolution of genetic variance along relatively steep gradients, as reflected by uneven cline spacing, and a large contribution of linkage disequilibria to genetic variance where finite margins are generated. In situations where the environment changes over a comparable scale to dispersal, population genetic factors are likely to be of great importance in generating limited ranges in nature.

Does responding to multiple threat types favour general wariness?

B. Brilot, J. Read and M. Bateson

It is well understood how animals alter their behaviour in response to a specific threat such as a particular predator species. Less well understood is how they might alter their behaviour when the environment contains different types of threats, *e.g.* terrestrial and aerial predators. General 'wariness' might be favoured, whereby levels of high risk for one threat favour a high level of responding to all other threats. There is still uncertainty as to what the optimal level of wariness might be and what factors might cause differences between species. This conundrum has parallels in the study of anxiety as an emotional process that modulates attention to threat. Should anxiety generated by one stimulus translate into an elevated response to others, what circumstances might favour this? We present a model based on signal detection theory that incorporates two threat types that contribute varyingly to two signals. The actor can respond to a particular received signal with one of two appropriate active responses or with a passive response (*e.g.* continuing to forage). In exploring the parameters of this model we can predict situations where generally high levels of responsiveness to all signals might be induced by signals from only one threat. Conversely we can also predict when enhanced risk from one threat-type should have no impact on responsiveness to cues that derive from an alternate threat.

Evolutionary models on graphs

M. Broom and J. Rychtar

There is a growing interest in the study of evolutionary dynamics on populations with some non-homogeneous structure. In this talk we investigate the case of non-directed equally weighted graphs and find solutions for the fixation probability of a single mutant in two classes of simple graphs. We further demonstrate that finding similar solutions on graphs outside these classes is far more complex. We investigate our chosen classes numerically, and discuss a number of features of the graphs; for example we find the fixation probabilities for different initial starting positions and observe that average fixation probabilities are always increased for advantageous mutants as compared against those of unstructured populations. Finally we discuss the extension of the model to consider evolutionary games on graphs.

Joint evolution of multiple social traits - an inclusive fitness analysis

S.P. Brown and P.D. Taylor

General models of the evolution of cooperation, altruism and other social behaviours have focused almost entirely on single traits, whereas it is clear that from humans to microbes, social traits commonly interact. Using an extension of inclusive fitness theory, we develop a general framework for the evolutionary study of social behaviours in multiple dimensions. We show that whenever there are interactions among social traits (whether ecological, genetic, chemical, physical), new behaviours can emerge that are not predicted by one-dimensional analyses. For example, a prohibitively costly focal cooperative trait can ultimately be favoured due to initial evolution in other (more permissive) social traits that can in turn change the effective cost-benefit ratio of the focal trait. We illustrate our framework with an analysis of the generic two-dimensional social dilemma posed by first, the construction and secondly, the exploitation of a shared public good. We find that, contrary to the separate one-dimensional analyses, evolutionary feedback between the two traits can cause an increase in the equilibrium level of selfish exploitation with increasing relatedness, while both social (production plus exploitation) and asocial (neither) strategies can be locally stable. If time permits, we will further extend the multi-trait social evolution framework with a theoretical and bio-informatic analysis of bacterial social evolution, mediated by horizontal gene transfer.

Founder mixing, inclusive fitness and the evolution of social behaviour in aphids

J. Bryden and V.A.A. Jansen

It is puzzling why clonally-reproducing aphids show less social behaviour than other haplo-diploid insects such as the Hymenoptera. Also puzzling are studies showing social aphids with high levels of mixing, due to inter-colony migration, between aphid colonies. Social behaviour, such as colony defence, housekeeping and gall repair, is commonly found in the 10% of aphid species that form communal nests in galls. The current broad spectrum, and multiple historical origins and losses, of aphid social behaviour suggest that sociality in aphids is adaptive. To clarify how selection operates in aphids, and to disentangle direct and indirect fitness components, we present a model of the life cycle of a typical colony-dwelling aphid. The model incorporates ecological factors and includes a trade off between investing in social behaviour or investing in reproduction. Our focus on inclusive fitness contrasts with previous approaches which optimise colony output. Through deriving a form of Hamilton's rule, we show that varying levels of colony-founder mixing, due to harsh environmental conditions, can explain a broad range of social behaviour. Founder mixing can be quantified using a standard relatedness measure, where high relatedness indicates little mixing. The costs and benefits of social behaviour are competition within the colonies and extra production from colonies respectively – both empirically measurable terms. Our model also shows how mixing due to realistic levels of inter-colony migration is unlikely to have a significant impact on the level of social behaviour.

Linking plankton dynamics and stochastic fish recruitment models

J. Burrow

Fish larvae live in an extremely variable environment. They are small relative to the spatial scales of prey heterogeneity and to the turbulent fluid flow at these spatial scales; they have only a local knowledge of their immediate environment, limited by a visual perceptive distance of around one body length; and they are subject to massive mortality, with a newly hatched individual's probability of survival to metamorphosis being O(1%) or less, driven by typical mortality rates of 10% per day in the larval stage. Because the key natural phenomena are inherently stochastic, deterministic models are likely to be inappropriate for quantifying recruitment. However, the usual stochastic modelling approach, which assumes that individual-based variability can be captured at the population level by a diffusion equation, may not be universally suitable. In particular, diffusion-based models cannot necessarily capture sudden jumps in growth caused by rare encounters with favourable patches of prey, or turbulent effects. Lévy process based models provide the necessary mathematical extensions to capture these jumps. Initial work has extended simple diffusion-based models of larval growth to Lévy jump-diffusion models, and has examined the consequences for recruitment probabilities [1]. Here we develop an explicit coupled stochastic model of larval-zooplankton-phytoplankton interactions, with the aim of exploring the roles of temporal matching of spawning and prey abundance, and prey heterogeneity and foraging strategies on the relationship between stock and recruitment.

[1] J. F. Burrow, P.D. Baxter and J.W. Pitchford (2008): Lévy processes, saltatory foraging, and superdiffusion. Math. Mod. Nat. Phenom., 3(3):115-130.

Models, metaphors, and the interpretation of fitness landscapes

B. Calcott

Recent work on fitness landscapes models suggests that the visual metaphor of landscapes has misled us, and the problem of peak-shifting is non-existent. A closer look at the use of models on which these arguments are based reveals a more complex story. Rather than discarding metaphors, the key move has been the use of multiple related models, where the results from one model justify the assumptions of another. Broad claims about the status of fitness landscapes requires a more careful interpretation of both how models relate to the world, and how they relate one another.

Populations level effects of grey seals (*Halichoerus grypus*) on the abundance of Southern Gulf of St Lawrence Atlantic cod (*Gadus morhua*)

A. Caskenette

The Gulf of St. Lawrence is a semi-enclosed sea on the eastern coast of Canada, connected to the Northwest Atlantic by the Strait of Belle Isle and Cabot Strait, and is naturally divided into southern and northern Gulf regions by the Laurentian Channel. The population of Atlantic Cod (*Gadus morhua*) in the southern Gulf declined in abundance in the 1990s, and is now at a record low. In contrast, the Northwest Atlantic Grey Seal (*Halichoerus grypus*) population has increased six fold since the termination of culling programs in the 1980's, and has been implicated in the lack of recovery for the Atlantic Cod. This implication has yet to be evaluated by scientific research; this study is the first to examine a range of population interactions between the two species. Several competing biological hypotheses for these interactions were developed, based on surveys of relevant literature and expert opinion. Three hypotheses (Aggregation Hypothesis, Belly-Biting Hypothesis, and Foraging Restriction Hypothesis) were quantified as separate mathematical models, with the most likely ecological interaction determined by the best fitting model according to its Akaike's information criterion (AIC) value. The major findings of this research were: (1) model selection can be successfully employed in a two-species population analysis of parsimoniously-effective combinations of sub-models; (2) the Aggregation Hypothesis as a univariate model holds the greatest potential for understanding Atlantic Cod-Grey Seal interactions in the southern Gulf.

Evolutionary, ecological, and life history consequence of the correlations of selection between and within habitats in heterogeneous environments

D. Cohen

1. Most natural populations experience different sequences of selective conditions at different frequencies of habitat types. 2. The force of selection at any one condition in any particular habitat type is proportional to the fraction of the total reproductive output at this condition. 3. The total force of selection on any one trait is defined by the weighted mean of the selection forces at all the conditions. 4. The force of selection at any one condition includes also the effects of positive or negative correlated selection in all the other habitats and conditions. 5. Two important consequences are modeled and analyzed: 5.1 The forces of selection and the predicted levels of adaptation in different habitat types may be very different in different habitats. Higher levels of adaptation are predicted in more abundant or productive habitats, while lower levels of adaptation are predicted in rare and less productive habitats. Adaptations at positively correlated habitats reinforce each other. 5.2 The forces of pre reproductive selection at the different conditions in the sequence in the same habitat patch are identical, and are proportional to the fraction of reproductive output at the habitat or patch. Low adult reproductive output will cause low levels of adaptation at all the previous conditions in the particular sequence. 5.3 Such back propagated effects may explain the evolution of unanticipated low adaptation at many conditions in natural environments.

The emergence of drug-resistant tuberculosis

C. Colijn, A.J. Ganesh, T. Cohen and M. Murray

Tuberculosis causes approximately 1.7 million deaths annually worldwide, and while global incidence is declining, TB incidence and mortality have risen dramatically in some locations. The emergence of highly drug-resistant TB strains plays a significant role in this rise, and in fact extensively drug-resistant (XDR) TB has now been found in over 50 countries, with some isolates are resistant to as many as 10 antibiotics. Drug resistance in TB is believed to arise mainly by chromosomal mutations, each occurring with very small probability per cell division and producing resistance to a single drug, so the quite rapid evolution of such widespread resistance to so many agents is surprising. We present a mathematical model of the growth of an initially drug-sensitive TB infection. Mutants resistant to a single drug arise randomly during the growth of the infection and give rise to their own populations of clonal descendants. We ask the relatively simple question: how many mutants are there when the population reaches a detection size? This question is complex in and of itself, but sheds some light on the emergence of multiple resistance and ultimately XDR-TB. We show that the distribution of the number of single mutants has very long tails, with the relative fitness of the mutants determining the tail of the distribution. This, together with the relatively high mean mutant numbers, leads to the likelihood of dual resistance being far higher than has previously been estimated, even before any treatment is initiated. Perhaps more fundamentally, if a resistant strain were transmitted caused a new infection, then the same reasoning we have used for the population of singly-resistant cells would apply to the population of dually-resistant cells in this new infection. Dual therapy would be expected to fail, resulting in a triply-resistant infection. In this way, transmission of resistant strains in combination with selective pressure applied to diverse cell populations in the host can serve to greatly amplify drug resistance. We conclude with a discussion of data on sequential drug resistance testing of TB infections, in which the in-host evolution of drug-resistance can be observed.

Evolution of stakeholder decisions in animals

L. Conradt

Social animals, just like humans, routinely make collective decisions. They collectively decide about communal movements, activities, nesting sites and enterprises, such as cooperative breeding or hunting, that crucially affect their survival and reproduction. In humans, collective decisions are often constraint by moral considerations (*e.g.* fairness, justice or the achievement of the greatest 'social welfare'). One way of achieving 'fair' collective decisions is to use weighted majority voting with weights proportional to stakes. A common example are company decisions in which stakeholders receive voting weights according to the proportion of their company shares. In contrast, animal collective decisions are subject to natural selection rather than moral considerations, and, on first sight, there does not seem to be an incentive to use weighted majority voting in order to maximize group-level welfare. However, in the present paper, I will show that under certain, common conditions individual-level natural selection can lead to the evolution of weighted decision making that is very similar to the weighted decision making aspired to by social welfare considerations. In particular, if individuals face trade-offs between (i) group fragmentation risks; and (ii) influencing group decision outcomes in their own interest. In such circumstances, purely selfish behaviour by individuals can result in group-level decisions that are close to those suggested by social choice theory in order to maximise group-level welfare. These results also shed interesting light on the possible evolutionary origins of human 'fair' decision making.

Stochastic models of plant growth and competition

S. Croft

Plants grow by investing resources in root production in order to capture nutrients from the surrounding soil. With heterogeneity in the environment (in both soil structure and nutrient distribution), a plant must proliferate its roots so as to maximise its chances of survival. The addition of competing neighbours makes this a race for limited, stochastically distributed resources. Deterministic models cannot capture the variation that occurs in such a system. Existing work [1] can describe observed size hierarchies in a controlled environment through an SDE based model. However, such models offer no insight into the underlying biological and environmental processes. By using idealised SDE drift-diffusion and stochastic-environment based drift-jump models, investigation into the effect of multi-scaled stochasticity on size hierarchies is underway. Using both analytical and computational approaches, the aim is to offer insight into size hierarchies in a system of competing plants within a stochastic environment, and to quantify the contribution of different evolutionary and ecological factors.

[1] Lv, Q., Schneider, M.K., Pitchford, J.W. Individualism in plant populations: Using stochastic differential equations to model individual neighbourhood-dependent plant growth. Theoretical Population Biology 74, 2008, 74-83

Microsatellite heteroplasmy maintained by selection mutation balance

H.P. de Vladar and J. B.W. Wolf

Most models of microsatellite evolution approach the subject of heteroplasmy assuming neutrality. We introduce a modification of the step-wise Markov model that accounts for selection (directional or stabilizing) for both the length of a microsatellite and its composition, that is the relative frequency of the core motifs appearing in an allele. To make the problem tractable, we study the equilibrium of these two variables in a population. The distinct types of selection have characteristic signatures that allow the identification of the selective scenarios. Namely, if the mutation probability and slippage rates are sufficiently low, the patterns of the genetic variance and the mean of the population's length distribution and motif frequency are distinct under different selective patterns. Otherwise, neutrality is approached, and the distribution of alleles is entirely determined by the mutation process. We corroborate our models with individual based simulations and molecular data.

Genetic architectures for quantitative traits

H.P. de Vladar and C. Watkins

There are many ways in which a quantitative trait (essentially a real number) could be encoded in a genome. In quantitative genetics the usual – indeed, nearly universal – assumption is that the trait value is the sum of the allelic effects at a number of loci: we term this a 'linear' encoding. We describe a variety of non-linear encodings with different and in some respects superior properties to linear encodings. We believe that some of these non-linear encodings have not previously been suggested. We assess the quantitative trait encodings according to the range and precision of the value that can be encoded, and the rapidity with which the encoded value can be altered by selection. We consider the response of the encoding to stabilising selection: that is, whether the precision – the intra-population variance – of the encoded values can be altered by stabilising selection. Finally, we consider the stability of the encoding under variations in population size. The implication of this work is that it is possible that the genetic architectures of quantitative traits may be more various than is often believed: the next step will be to consider the evolutionary stability of non-linear genetic encoding systems themselves.

Survival of bumblebee nests in a complex landscape

M. Devoto and J. Memmott

Food resources available to insects change in space and time. These changes might affect the spatial distribution of insect populations throughout a given landscape. We use information from a recent study in Caledonian pine forests to model the patterns of distribution of bumblebees in response to spatial variations in resource availability. Bumblebees are constrained to forage within flying distance from their nests, which makes them particularly sensitive to changes in the availability of resources within their fixed foraging area. Results suggest that both the spatial distribution of resources and their availability at different times throughout the season are crucial to explain the pattern of distribution of bumblebee nests in a given landscape. This has significant implications for the successful restoration and long-term conservation of these key pollinators.

The modelling of fimbriation in *Escherichia coli*

P. de Vries

The virulence of *E.coli* is expressed through its fimbriae. Fimbriae are the hair-like attachements on the outside of the cell, used to attach the cell to specific sites on the host. Only a small fraction of the cells form these fimbriae, but all cells benefit from the nutrients released by the host because of the stimulation of the host and the subsequent release of nutrients. Over time most *E.coli* bacteria seem to have found a good optimum for different hosts where they manage to avoid overstimulating the host and triggering all defence mechanisms and receiving their nutrients. Little is understood about the processes involved due to the large amount of interrelated processes and protein interactions. The main part is a piece of DNA of 314 base pairs in length that with the help of two different proteins is removed and inserted in such a way that the transcription of the fim operon can take place (ON) or to switch the transcription OFF. The processes involved in either stimulating production of FimB (OFF-to-ON) or FimE (OFF-to-ON) are interconnected with many other processes in the cell and are tied in with many systems to do with cell survival. For this reason we build a set of computer models (one based on differential equations and one agent based stochastic model) to predict fimbration based on these processes. Once complete this model can be used to investigate the evolutionary advantages of having such a complex regulatory system. The aim of this poster is to describe process of creating the computer model and to give a few initial hints in how certain processes evolved, based on the results from these different models.

Modelling social foraging and resource predictability in the case of vultures

C. Deygout, O. Duriez, F. Sarrazin and C. Bessa-Gomes

Whether foraging individuals use social information or personal information derived from their previous experience should largely depend on resource predictability. In particular, when resources are unpredictable, personal information may be of little use, as illustrated by scavengers such as Gyps vultures that largely rely on social foraging strategies. But resource predictability may change because of human activities. For example, the use of feeding stations makes food patches more predictable, affecting the very nature of the available resources. We explored the impact that different predictability levels of food resources might have on foraging strategies, in particular on the use of personal versus social information. We developed an individual-based spatially explicit model of foraging Gyps vultures in presence of feeding stations to explore different behavioural hypotheses as well as different management scenarios. When resources were predictable, individuals using previously acquired personal information (‘Trapliners’) were more successful that those relying on social information (‘Networkers’). The situation was reversed when there were no or too little predictable resources. Local enhancement, another form of social information available to all strategies, did not appear to benefit Trapliners. Trapliners were more aggregated than Networkers and suffered more dearly from competition on the food resources. Even when some resources are predictable, Trapliners were not more successful than other strategies in large populations.

Limited dispersal helps preserve genetic polymorphism in coevolving plant-pathogen recognition genes

S. Dobbie

Polymorphism in matching plant-pathogen immunity-antigenicity genes is common and in many cases extremely ancient. Theoretical studies have shown this long-term stability requires direct negative frequency-dependent selection, such that one or more of the genotypes involved becomes less fit as it grows more common. This can be generated by several ecological or epidemiological details, including variable disease prevalence. Simple non-spatial models show this, but do not reflect the spatial details of real-world host-parasite systems. We have developed a spatially explicit individual-based model in which limited dispersal leads to spatial structure. This leads to local clustering of genotypes, which favours the generally rarer genotypes in this system. Globally, limited dispersal leads to reduced connectivity between regions. Both of these factors further strengthen long-term stability of polymorphisms.

Behavioural attainability of evolutionary stable strategies in repeated interactions

R. Dobler

Theory for the evolution of social interactions based on continuous strategies often assumes for simplicity that expressed behaviours are independent from previous encounters. In reality, however, such dependencies are likely to be widespread and often strong, generating complex behavioural dynamics. To model this process and illustrate potential consequences for the evolution of behavioural interactions, I consider the behavioural dynamics of the interaction between caring parents and their demanding offspring, a prime example for long series of interdependent and highly dynamic interactions. These dynamics can be modelled using functions describing mechanisms (reaction norms) for how parents and their offspring respond to each other in the interaction. This way the general conditions under which the behavioural dynamics converge towards a proximate equilibrium can be established and I refer to such converging interactions as behaviourally stable strategies (BSSs). I further demonstrate that there is scope for behavioural instability under realistic conditions; that is, whenever parents and/or offspring 'overreact' beyond some threshold. By applying the derived condition for behavioural stability to evolutionary models of parent-offspring conflict resolution, numerical simulations show that evolutionarily stable strategies (ESSs) of current models are not necessarily behaviourally stable. Because behavioural instability implies that expressed levels of behaviours deviate from the ESS, behavioural stability is required for strict evolutionary stability in repeated behavioural interactions.

Mathematising Darwin

A.W.F. Edwards

Although the first mathematical account of one of Darwin's evolutionary arguments actually occurred before the introduction of Mendelian genetics in the early years of the twentieth century, real advance only came with what Ernst Mayr called 'the Fisherian synthesis', in which R.A. Fisher, principally through his 1930 book *The Genetical Theory of Natural Selection*, brought together Mendelian theory and Darwinian evolution, dispelling the doubts that many biologists of the time had about the sufficiency of Mendelism as an explanation. Fisher's synthesis will be compared with the later and more analytical contributions of J.B.S. Haldane and Sewall Wright, and some concluding remarks made about the second part of 'the evolutionary synthesis' dominated by the books of Huxley, Dobzhansky, Simpson and Mayr.

What to do first: grow or reproduce? Evolutionary dilemma of indeterminate growers in the seasonal environment

M.J. Ejsmond, M. Czarnołęski, F. Kapustka and J. Kozłowski

We use dynamic optimization algorithm to find adaptive schedules of energy allocation to growth and reproduction in the seasonal environment. Value of newborns in our model is related to the timing of reproduction. We show that this assumption changes the way in which organisms allocate resources to growth and reproduction from the first-grow-then-reproduce mode, commonly predicted by previous models, to the first-reproduce-then-grow or first-grow-then-reproduce-then-grow mode of resource allocation. Reproduction preceding growth in seasonal breeders with indeterminate growth is often observed in fishes, amphibians, reptiles and mollusks but so far has not been predicted by optimization theory. We also showed that devaluation of offspring production provides favorable conditions for the evolution of capital breeding, even in fully predictable seasonal environments. Our results suggest that studies on optimality of capital versus income breeding have to consider the dependence of offspring value on its birth date in a season.

A plant-pollinator model with complex life cycles

F. Encinas-Viso, D. Alonso and R.S. Etienne

Plant-pollinator interactions are among the most ubiquitous mutualistic interactions. Various theoretical models have been constructed to understand the dynamics of this interaction. An important feature of plant-pollinator interactions is that most insect pollinators and plants have different life-stages. The inclusion of complex life cycles (CLC) seems to better describe the dynamics of other ecological interactions, such as host-parasitoid and predator-prey interactions. To our knowledge, the incorporation of CLC into the dynamics of plant-pollinator interactions has not yet been considered. We developed a simple two-stage-structured model of a mutualism between a population of plants (plants and flowers) and a population of obligate insect pollinators (larvae and adults) to describe the dynamics of this interaction. Our model shows that stability and coexistence depend on a set of life-history parameters that reflect the viability of an individual (maturation rate, birth rate and death rate), but also the efficiency of pollination and intraspecific competition. Obligate pollinators that have a low basic reproductive ratio can still persist and coexist if (1) their densities are above the extinction threshold due to a strong Allee effect, (2) they are efficient pollinators and (3) they can resist strong competition.

Sperm in competition: sperm quality and survival

L. Engqvist

When females mate with more than one male, a male's reproductive success will to a large extent be determined by the fertilization success of his sperm. In this highly competitive situation, sperm with reduced capacity will only have minute chances to fertilize an egg cell. Genetic changes causing a decrease in semen quality should therefore be rapidly swept away by selection. At odds with this view are many studies demonstrating variation in sperm viability traits in natural populations. Why don't males manufacture sperm of the highest possible viability? One reason might be that producing highly viable sperm is costly. It has repeatedly been suggested that the benefit of high sperm viability should be greatest under the most intense sperm competition, but empirical observations show relatively high levels of sperm inviability, even in promiscuous mating systems with high levels of sperm competition. To make sense of this, we need theoretical analyses of sperm competition which explicitly incorporate variation in sperm quality. In particular, we need to consider temporal effects in sperm competition dynamics, especially in systems with prolonged female sperm storage, in order to better understand how selection shapes investment in sperm viability and survival. Here I will present first results from an evolutionary invasion analysis focusing on the evolution of sperm quality, defined as the survival rate of sperm. These results indicate that in contrast to the general view, increased sperm competition intensity will in many cases lead to an increased level of sperm mortality.

The allometry of diversification

R.S. Etienne, S.N. de Visser, H. Olff et al.

One of the most striking patterns observed among animals is that smaller taxa are generally much more diverse than larger taxa. Classic macroevolutionary explanations state that net diversification rates must be smaller for large animals, either because the speciation (origination) rate declines with body size, or because extinction rate increases with body size (or both). Here we develop a new mechanico-statistical method to reveal the underlying allometries of speciation, extinction and diversification from diversity data, combining the prevailing stochastic birth-death model of diversification with allometric relationships. We applied this method to a data set of a wide range of taxa within the Metazoa (from insects to mammals) compiled from the literature. We find that the higher diversity among small animals is due to different mechanisms than previously assumed.

Learning your own strength: winner and loser effects should change with age and experience

*T.W. Fawcett and R.A. Johnstone**

Models of animal conflict typically assume either that individuals do not differ in fighting ability, or that they are fully aware of any such differences. How should conflicts be resolved when individuals do not know their own strength directly? Here we model a population of strong and weak individuals that meet at random and compete over resources by playing a simultaneous Hawk-Dove game in which stronger individuals have an advantage. Individuals are unaware of their own strength, but keep track of the number of escalated fights they have got into and how many of those fights they have won. Using dynamic programming, we identify the evolutionarily stable strategy (ESS) for aggression. Under the ESS, individuals show clear winner and loser effects: those winning fights are more likely to escalate subsequent conflicts, whereas those losing fights retreat from aggressive opponents. However, these effects are strongly dependent on age and experience. Young, naïve individuals show highly aggressive behaviour and pronounced loser effects. For these inexperienced individuals, engaging in fights entails a fitness benefit purely in terms of information, aside from any potential gains in terms of resources. As they mature and gain experience, the level of aggression declines, with individuals losing fights switching to more Dove-like behaviour. Older individuals, which have a better idea of their own strength, are more strongly influenced by victories than losses. We suggest that age-dependent patterns of aggression may result from changes in how individuals perceive their own strength.

Predicting optimal offspring size when adults and juveniles do not occupy the same niche

B. Fischer, H. Kokko and B. Taborsky

Offspring size is a trait that can have a strong effect on fitness, as larger offspring are often documented to have a survival advantage under harsh environmental conditions. Selection should hence favour mothers that find an optimal solution to the offspring size vs. number trade-off. If environmental conditions are variable, there will not be a single optimal offspring size, as typically predicted for constant environments. Instead, mothers are expected to make plastic decisions regarding offspring size. To be able to adjust offspring size in an adaptive manner, mothers have to use cues available to them to predict offspring environmental conditions. This task becomes considerably more complex in species where individuals occupy different niches at different life stages such that the juvenile and adult environments are separated. Here, we present a conceptual model to investigate plasticity in offspring size in a stochastic environment where juvenile and adult environments are not identical and vary stochastically. We investigate how optimal plasticity in offspring size might vary with a mother's predictive ability of juvenile environmental conditions, and how the reliability of cues available to a mother might hence influence the evolution of phenotypic plasticity in offspring size.

Rapid evolution makes culture adaptive

M. Franz and C.L. Nunn

Culture is widely thought to be adaptive when social learning is less costly than individual learning. In radical departure from this view, Rogers (1988) showed that social learning does not necessarily improve the fitness of the population in the long term. This has come to be known as "Rogers' paradox." To derive an analytical solution for the dynamics of his model, Rogers assumed that genetic evolution is much slower that cultural evolution. However, this assumption might not be well justified in light of accumulating findings of rapid evolution in biological systems. Using simulation experiments, we reanalyzed Rogers' model after relaxing the assumption that genetic evolution is much slower than cultural evolution. Our results show that this assumption is crucial for the emergence of Rogers' paradox. For many parameter settings, genetic and cultural evolution occur on the same time scale, and feedback effects between both genetic and cultural dynamics can increase the mean fitness of the population. In contrast to Rogers' finding, this result shows that by avoiding the costs of individual learning, social learning can increase the fitness of the population without relying on complex learning strategies. Slow genetic evolution is often assumed in models of social evolution. As demonstrated by our results, this assumption might impede the discovery of important evolutionary dynamics.

Detecting anomalous diffusion in animal movement

L. Giuggioli

Understanding behaviour from animal movement relies heavily on how the statistical features of movement trajectories can be well characterized. This detection aspect has become increasingly important as the sophistication of the modelling tools has grown dramatically. One such example is the mathematical framework of anomalous diffusion which has entered the arena of animal ecology since Lévy movement strategies have been shown to optimize target encounter rates of naive searchers under certain conditions. A description of some of the anomalous diffusion models and useful methods to parameterize them will be followed by an application to satellite tracking data about shearwaters (*Puffinus mauretanicus* and *Calonectris diomedea*) foraging in the NW Mediterranean. It is shown how, in presence of fishing activity (trawling boats), the shearwaters perform area-restricted search, whereas, in the absence of fishing activity, movement characterized by very long distance displacements appear evident.

Defense, intrusion and the evolutionary stability of territoriality

M. Hinsch

In territorial populations space is partitioned between individuals in the sense that every individual only has access to a very limited area and the resources therein. Very little is known about why this partitioning takes place and how it is maintained by selection. Analysis of a simple mathematical model suggests that resource partitioning can be evolutionarily stable if fighting costs are low for owners and high for intruders and if individuals move slowly between territories. Using a more detailed individual-based simulation model however we find that non-equilibrium resource dynamics usually lead to the disappearence of territoriality. Resource partitioning can only be maintained if fighting costs for the intruder relative to the productivity of the territory are very high or if movement between territories itself carries a substantial cost.

The origins of lactase persistence in Europe

*Y. Itan, A. Powell, M.A. Beaumont, J. Burger and M.G. Thomas**

Lactase persistence (LP) is common among people of European ancestry but, with the exception of some African, Middle-Eastern and southern Asian groups, is rare or absent elsewhere in the world. Modern DNA evidence indicates that this trait is caused, in Europeans, by a single mutation that arose in the last 12,000 years, has evolved independently multiple times in Africa, and has been the target of strong natural selection. Furthermore, ancient DNA work has shown that LP was very rare or absent in early Neolithic central Europeans. It is unlikely that LP would provide a selective advantage without a supply of fresh milk and this has lead to a gene-culture co-evolutionary model where lactase persistence is only favoured in cultures practicing dairying, and dairying is more favoured in lactase persistent populations. We have developed a flexible demic computer simulation model to explore the spread of lactase persistence, dairying, other subsistence practices and unlinked genetic markers in Europe and Western Asia's geographic space. Using data on LP variant frequency and farming arrival dates across Europe, and approximate Bayesian computation to estimate parameters of interest, we infer that the LP first underwent selection among dairying farmers around 7,500 years ago in a region between the central Balkans and central Europe, possibly in association with the dissemination of the Neolithic Linearbandkeramik culture. Furthermore, our results suggest that natural selection favouring a lactase persistence variant was not higher in northern latitudes through an increased requirement for dietary vitamin D.

The evolution of leaders and followers

R.A. Johnstone and A. Manica

When members of a group disagree over their preferred course of action, coordination can be hard to achieve. Recent experimental work on pairs of foraging sticklebacks has shown that individuals may differ consistently in their tendency to adopt the roles of leader and follower. Here, I present a simple model to account for the evolution of such temperamental differences. I consider two players engaged in repeated play of the Battle of the Sexes game, in which each may choose between two options; both gain a positive payoff only if they make the same choice, but each prefers a different option. I assume that individuals may vary in their tendency to 'lead', *i.e.* to choose their own preferred option, rather than to 'follow', *i.e.* to copy the other player's last choice. I then show that in this simple game, selection leads to repeated evolutionary branching and strategic diversification, giving rise to highly polymorphic populations. Diversity is favoured because high levels of coordination are achieved only when a pair comprises a clear leader and a clear follower. Within a polymorphic population, leaders tend to gain a relatively greater payoff than followers with whom they are paired, because the pair more often coordinate in following the course of action favoured by the leader. At the same time, however, leaders experience lower levels of coordination on average due to the risk of being paired with other leaders. Strategic diversity is thus maintained by frequency-dependent selection.

Language shift, bilingualism, and the future of Britain's Celtic languages

A. Kandler

In this paper we model the dynamics of language shift as a competition process in which the numbers of speakers of each language and of the bilingual sub-population vary as a function both of internal recruitment (as the net outcome of birth, death, immigration and emigration rates), and of gains and losses due to language shift. We apply our approach to the English-Gaelic competition in Western Scotland. We are able to replicate the main dynamic of the shift process and give predictions about the future of the Gaelic language under unchanged environmental conditions. Contrary to the Gaelic situation where a sharp decline of the number of Gaelic-speakers is observable the Welsh situation is an example of a remarkable revival of an almost moribund language. The revival success is related to strategies whose objective is stable societal bilingualism - by creating or preserving segregated and complementary sociolinguistic domains, in each of which one or other language is the preferred medium of communication. To consider these effects we examine a second model in which bilingualism is no longer simply the transitional state. Superimposed on the basic shift dynamic there is an additional demand for the endangered language as the preferred medium of communication in some restricted sociolinguistic domain, and this demand persists until the number of speakers of the endangered language becomes very small (at which point the demand ceases). We present numerical case studies for both, the English-Gaelic and English-Welsh competition.

Different networks with identical clustering: implications for disease dynamics

I.Z. Kiss and D.M. Green

We consider previously proposed procedures for generating clustered networks [1, 3, 4] and investigate whether and how these procedures lead to changes in network properties other than clustering. Based on these procedures, we generate networks and use different network measures to characterise their structure. For high levels of clustering, the procedure proposed by Newman [3] leads to networks with higher degree heterogeneity [2] while networks based on the procedure proposed by Read and Keeling [4] are assoratatively mixed ('like attaches to like'). For different networks, but with the same clustering, we interpret our findings in terms of the impact of the network structure on disease outbreak threshold and disease dynamics.

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Evolution of the two sexes

H. Kokko, M.D. Jennions and J. Lehtonen

Sexual selection is often called Darwin's 'other' theory. While Darwin laid the foundations of the study of the two sexes, he did not ask why the two sexes exist in the first place. Nowadays we know that sexual reproduction often leads to anisogamy: one mating type evolves much smaller gametes than the other and is thereafter called the male sex. Explaining why the two sexes diverge in numerous other traits too is a central question of current sexual selection theory. Since a seminal contribution by Trivers (1972) we have known that differences in parental investment between the sexes are a key factor in this analysis. It is, however, still perhaps underappreciated how convoluted the evolution of this difference is. Firstly, as already pointed out by Dawkins and Carlisle (1976), one must avoid the 'Concorde fallacy' when predicting that the sex that has invested more so far is selected to keep investing more. We also show that the field is littered with other predictions that appear intuitive but are, in fact, not sound. The simple biological fact that each offspring (in diploid species) has one genetic parent of each sex produces frequency-dependent selection on care that strongly resembles frequency-dependent selection on the primary sex ratio. We will discuss why this frequency-dependence nevertheless does not produce egalitarian sex roles while it strongly promotes equal primary sex ratios. We will also ask whether the selective forces that lead to anisogamy itself are well enough understood.

Decision making and the evolution of mental laziness

K. Koselj and B.M. Siemers

To decide adaptively animals have to estimate parameters of their environment. High environmental variability and complexity make an accurate judgment a demanding and time-consuming task. Moreover, cognitive processing is highly costly in terms of energy consumption, processing time and recovery, making a completely accurate decision less profitable. We modelled a decision maker that decides whether to accept or reject encountered items (*e.g.* prey) based on previous experience. During the decision process accuracy of judgment is traded off against cognitive effort. The model predicts that environmental variability and complexity on one hand and high cost of cognitive processing on the other facilitate the evolution of mental laziness as a homeostatic neural regulator. The cost of erroneous decision is dependent on body reserves. To test these predictions, we conducted prey selection experiments with greater horseshoe bats in the laboratory. In accordance with our model, the behaviour of bats shows that the effort they invested in decisions was correlated with their body reserves and the complexity of the foraging environment.

Lac operon: An example of evolutionarily optimized molecular switch?

V. Krivan

It is well know that in mixed substrates with glucose and lactose bacteria often utilize glucose first and then switch to lactose (or to some alternate source of energy). At the molecular level this switch is known as the lac operon. In this talk I ask: Is this switch evolutionarily optimized? In other words, do bacteria switch between the resources at the time that maximizes their fitness? To answer this question I build a model of bacterial growth on two substrates. The model assumes adaptive bacterial switching that maximizes bacterial per capita population growth rate - a proxy for bacterial fitness. Using some data from the literature, this model allows me to predict the time at which bacteria should switch. Then I compare this predicted time with observed times of switching for different substrates and different initial concentrations. The observed times of switching show a good agreement with predicted times. This supports the idea that the molecular mechanism regulating resource switching is evolutionarily optimized.

Inferring patterns of gene flow in Scots Pine using individual based models

D. Lawson

Spatial gene flow patterns are created by two types of forces: stochastic birth and death events, and deterministic factors such as selection. Scots Pine shows highly non-random spatial patterns in its genetic diversity as indicated by chemical markers called terpenes. Because it exists in an extended and heterogeneous environment it is tempting to conclude that the diversity is caused by the environmental covariates that correlate over its range. However, correlation does not imply causation and the correct null model for the variance structure of the trees is not captured by simple spatial patterns but a complex birth and death process capturing both the spatial and temporal correlation implied by shared heritage. We use such a biological 'null model' containing a stochastic birth-death process to investigate whether environmental covariates are required in order to explain spatial patterns of diversity in Scots Pine.

Crypsis, aposematism or a combination of both? - An optimisation model

T.J. Lee and M.P. Speed

Prey often adopt colouration as a means of defence against predators, whether in the form of crypsis, acting to reduce a prey's visibility against its background or aposematism, acting as a conspicuous warning signal advertising the prey's unpalatability to the predator. It is evident from observing the colouration patterns of animals that the two classifications may not always be mutually exclusive; animals often possess complex patterns which may contain elements of both cryptic and conspicuous patterns, making simple classification of a prey's appearance unclear. For example some caterpillars have a series of black and yellow stripes on their bodies and it has often been speculated that when viewed from a distance these two colours blend and help to make the animal cryptic, but when viewed from close up the colours are brightly aposematic Here we examine the idea that some combination of both crypsis and aposematism could be optimal for prey: maximising cryptic effects when predators are at a distance from prey but also serving as a warning signal to warn off predators at close proximity. We present the results of deterministic numerical optimization models which allow prey phenotypes to evolve to their optimal frequencies and report a range of plausible biological scenarios in which a combination of chemical defence combined with cryptic and aposematic elements of display can be optimal.

Constraints on adaptation: Explaining deviation from optimal sex ratio using artificial neural networks

H.M. Lewis

Determining the processes constraining adaptation is a major challenge facing evolutionary biology. We investigated if the evolution of suboptimal behaviour was due to information acquisition and processing by using artificial neural networks (ANNs). The model system was a solitary parasitoid wasp laying male offspring in small hosts and female offspring in large hosts, where theory predicts the switch should be instantaneous but is usually observed to be gradual. We found that simple ANNs were able to evolve fairly sudden switches in sex ratio and therefore the limitation in wasps is unlikely to be solely due to neural processing restrictions. Several additional constraints caused changes in sex ratio allocation; these included fitness costs to neural processing, variation in the host-size distribution and simplification of the internal ANN structure (smaller 'brain size'). None of the constraints affected the location of the switch from male biased to female biased, with the exception of the variable host-size distribution. Analysis of the functions determining fitness showed that the sharpness of the switch is less important to overall population fitness than the location of the switch point, explaining why the sharpness of the switch is more sensitive to information processing constraints than the switch point.

Learning about population history using an approximate Bayesian computation

J. Lopes and M. Beaumont

Approximate Bayesian Computation (ABC) is a recent developed Bayesian technique that can be used to extract information from DNA data. This method has been firstly introduced to population genetics in 1999 by Pritchard and co-workers. It relies in two major approximations: the use of a simulated step that substitutes the need for using an explicitly likelihood function; and the summarization of DNA data with a set of summary statistics. This Bayesian approach can be used to estimate several demographic historic parameters from populations using DNA data. A particular ABC method, similar to the one used by Beaumont (2007), was applied to published data of bonobos and chimpanzees (Won and Hey, 2005) that had been studied before using different flavours of MCMC (Becquet and Przeworski, 2007; Hey and Nielsen, 2007). Two other data sets of human populations from the Nicobar and Andamanese islands and Central Africa have also been studied. The ABC studies confirm the competitiveness of this recently explored Bayesian method when compared to a standard MCMC approach. Its potential role on phylogeography and demography researches is emphasized.

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Evolution and ecology of the market place: biology inspiring the management of computer systems

P. Marrow, P. Lewis and X. Yao

Evolution and ecology have shaped the natural world. They have also inspired computing research and applications. Biological evolution has inspired the field of evolutionary algorithms. Ecology has inspired the field of multi-agent systems. Each agent is an autonomous element of software, analogous to individuals in biological populations. A central topic in ecology is resource limitation and the competition that results; in human populations this has led to the market, where game theoretic analysis has led to important links with biology from economics. In computing applications resource limitation is also often an important issue, as multiple users and processes compete. In this work we draw inspiration from ecology in constructing computational populations in the form of multi-agent systems, where agents act on behalf of users. We reflect the problem of resource limitation in ecological systems by establishing a market in which agents can establish prices to buy and sell resources. We draw inspiration from Darwinian evolution in using evolutionary algorithms to identify the prices that agents offer to buyers. Our work is research towards an applied aim: how to manage computational resources over a distributed system where there is no central control on these (limited) resources? We analyse properties of this market using game theory and simulation. We show that the use of a market for resources where prices are set by evolutionary algorithms can lead to convergence to a stable state where resources are appropriately distributed according to demand, even though different agents may have different objectives.

The donation game with roles played between relatives

J.A.R. Marshall

We consider a social game with two choices, played between two relatives, where roles are assigned to individuals so that the interaction is asymmetric. Behaviour in each of the two roles is determined by a separate genetic locus. Such asymmetric interactions between relatives, in which individuals occupy different behavioural contexts, may occur in nature, for example between adult parents and juvenile offspring. The social game considered is known to be equivalent to a donation game with potentially non-additive payoffs, and has previously been analysed for the single locus case, both for discrete and continuous strategy traits. We present an inclusive fitness analysis of the discrete trait game with roles and recover equilibrium conditions including fixation of selfish or altruistic behaviour under both behavioural contexts, or fixation of selfish behaviour under one context and altruistic behaviour under the other context. These equilibrium solutions assume that the payoff matrices under each behavioural context are identical. The equilibria possible do depend crucially, however, on the deviation from payoff additivity that occurs when both interacting individuals act altruistically.

The effect of density-dependent nest destruction on the sex ratios of green turtles on Ascension Island

L. McNally, A.J. Jackson, J. Ellick, R. Frauenstein, B.J. Godley and A.C. Broderick

The Ascension Island population of green turtles (Chelonia mydas) has risen by 285% since the 1970's and is the second largest green turtle rookery in the Atlantic. With such a magnitude of population growth it is important to understand when and how density-dependent mechanisms will begin to limit this growth. One such potential mechanism is density-dependent nest destruction, which will affect recruitment but also has the potential to affect hatchling sex ratio. As females are usually the limiting sex regarding population growth a reduction in the number of females surviving to hatching will limit population growth. This study uses both analytical and simulation models to investigate the impact of density-dependent nest destruction on the sex ratios of hatchlings on Ascension Island. The results of the models show that though density-dependent nest destruction has a consistently masculinising effect on hatchling sex ratios this effect was negligible for the levels of nest destruction observed during the study period. The effect of loss of recruitment due to nest destruction is currently low, with only 1% of all nests deposited during the study period being destroyed by density-dependent nest destruction. However, this masculinising effect is shown to act in a density-dependent manner and will therefore increase for higher population levels. It is likely that as the Ascension Island population continues to increase the impact of density-dependent nest destruction will become a significant factor in regulating population growth, both through its direct effect on recruitment and its effect on hatchling sex ratios.

When is optimism optimal?

J.M. McNamara, P.C. Trimmer, J.A.R. Marshall, A.Eriksson and A.I. Houston*

We define optimism as behaving in a way that gives too much weight (in terms of the production of surviving offspring) to positive events, whereas pessimism gives too much weight to negative ones. Although optimism and pessimism seem irrational, we show that they can be favoured by natural selection. Natural selection does not necessarily act to maximise numbers of offspring or even grandchildren, but maximises an appropriate measure of the number of descendants left far into the future. As a consequence, natural selection may produce behaviour that seems irrational from a short-term perspective. We establish that the spatial and temporal structure of the environment determines whether optimism or pessimism is optimal. If stochasticity affects individual population members independently (for example because they are in different habitat types) and there is a positive correlation between circumstances experienced by parents and offspring, then optimism is favoured. If stochasticity affects all the members of a population in a similar manner (because of large-scale temporal fluctuations) then pessimism is favoured. We then combine different types of variability to identify the reason for an initially counter-intuitive result.

Spatial heterogeneity can modify the type of zooplankton functional response: a model study based on field observation

A.Y. Morozov

Parameterization of predation terms plays a crucial role in dynamics of food-web models. Theoretical studies predict enhancing of ecosystems' stability in case a functional response is of sigmoid type (Holling type III). The choice of a correct type of functional response is especially important for modelling stability of aquatic eutrophic ecosystems, where grazing by zooplankton often controls algal blooms. Extensive experiments on zooplankton feeding in laboratories, however, show non-sigmoid nature of responses for herbivorous zooplankton. As a consequence, we cannot implement Holling III type grazing in plankton models. I argue, however, that such an 'evident' claim is just wrong and sigmoid functional responses in real plankton communities would emerge more often than it was suggested earlier. I have conducted a rather extensive literature search on data of zooplankton feeding *in situ*. Moreover, I used field data obtained by my colleagues from the Shirshov Institute of Oceanology. Based on the collected data, I demonstrate that vertical heterogeneity in algal distribution as well as active zooplankton foraging behaviour can modify the type of zooplankton functional response. In particular, the rate of food intake by zooplankton often exhibits a sigmoid response, instead of a non-sigmoid one found previously in laboratory experiments for the same species. I show that this conceptual discrepancy is due to the ability of zooplankton to feed in layers with high algal density. I propose two conceptual models explaining the observed alterations of type of response. The models predict the crucial role of light attenuation by phytoplankton in the alteration of the functional response.

Patterns of patchy spread emerging in multi-species reaction-diffusion models

A.Y. Morozov

Spread of populations in space often takes place via formation, interaction and propagation of separated patches of high species density, without formation of continuous fronts. Such type of spread is called a 'patchy spread'. In earlier population models, patchy spread was considered to be a result of a pronounced environmental or/and demographic stochasticity. Recently, it was found that a patchy spread can arise in a fully deterministic predator-prey system and in models of infectious diseases. It is well recognized now that patterns of patchy spread in real ecosystems are a result of interplay between stochastic and deterministic factors. However, deterministic models of patchy spread are developed and studied much less compared to those based on stochastic mechanisms. As such, a further progress in understanding the role of deterministic factors would be extremely helpful. In my study, I implement the reaction-diffusion framework in two spatial dimensions in a homogeneous environment and demonstrate emergence of patchy spread in different multi-species population models. In particular, patchy spread arise both in mutualism and competition models influenced by predation. I demonstrate a pattern of patchy spread having significantly different speeds in different spatial directions in a fully homogeneous space. Earlier such phenomenon was attributed to strong environmental heterogeneity. The basic features of spatiotemporal dynamics of patchy spread common for all models are formulated. Finally, I mark out properties of the reaction' terms which are necessary for obtaining patchy spread based on the reaction-diffusion modelling approach.

The evolution of social coordination in humans

D. Nettle

There is a vast literature on how the cooperation between unrelated individuals which is so typical of humans can evolve, but much less attention has been paid to what kinds of social coordination arrangements will be found under what circumstances. In the ethnographic literature, one can find examples of communal sharing, where all resources go into a common pot with no book-keeping and no requirement for reciprocity, rotating credit associations, where individuals take turns to privatize the group's entire resource, status hierarchies, where high-rank individuals have preferential access, and many other arrangements. What determines which kinds of arrangements evolve under what conditions? We present a simple formal model with two key parameters, the extent of shared interest between individuals, and the shape of the fitness returns to consumption of the resource. Where there are high degrees of interdependence and/or diminishing fitness returns to consumption, there is little payoff for controlling the allocation of resources. An ESS analysis shows that communal sharing will evolve under these conditions, since as long as groups are small, the benefit of trying to monopolise the resource does not exceed the cost. Where returns to consumption are accelerating and interdependence is high, turn-taking is an ESS. Elsewhere, the population can be invaded by individuals who attempt to seize control of the distribution. We interpret the results in the light of the diversity of arrangements for distribution of resources across different societies.

Local adaptation in a changing environment

A. North

Empirical studies of spatially structured populations often reveal patterns of genetic and ecological divergence which are strongly correlated with geographical structure. Divergence may result from adaptive responses to spatially structured variation in habitat, so that resident genotypes in each deme should have on average a higher relative fitness in their local habitat than genotypes originating from other habitats. This pattern, and the process leading to it are known as local adaptation. However, local adaptation may be hindered by gene flow, confounded by genetic drift, opposed by natural selection due to temporal environmental variability, and constrained by lack of genetic variation or by the genetic architecture of underlying traits. This poster outlines a spatial and stochastic modelling framework we have constructed to investigate how dispersal, reproductive mechanism (sexual or asexual), landscape structure and habitat loss influence the balance between local adaptation and (generalist or plastic) global adaptation. Preliminary results show how populations are inclined to locally adapt in sparse and temporally stable landscapes, and that sexual reproduction encourages local adaptation.

Optimal foraging strategies in a random resource model

P. Nouvellet

Accurate description and simulation of animal movement is of crucial importance when investigating the strategies to optimally search and exploit food resources. In a recent publication, a model of correlated random walk was presented and, as well as describing with great accuracy ants individual movement, it allows realistic simulation of movement to be simulated. In contrast to previous approaches, which rather artificially described movements as occurring in a sequence of jumps, at random times and at random angles, our work realistically models movement as continuously occurring, as it indeed is, for a wide class of organisms (possible exceptions are rapidly jumping organisms, such as fleas and jumping spiders, which are not considered). The simulations developed are used in the context of foraging to explore and define a set of predicted strategies that appear optimal. Amongst the different life history characteristics, we focus our attention to central place vs. harvester strategies, group vs. solitary strategies and the sensory range of the individuals. The distribution of resource is also considered as a factor influencing the optimal strategy.

Group size depends on mutation rate in simulated altruistic vampire bats

M. Paolucci and A. di Salvatore

Evolution of altruistic behavior is one of the main puzzles of biological and cultural evolution. The puzzle is a consequence of the idea of evolution through natural selection and of the definition of altruistic behavior as having a fitness cost for the individual performing it. By definition, something that reduces fitness is selected against; ergo, no altruism can evolve in Darwinian terms. Biological and cultural evidence show the contrary; after a debate more than forty years long, and the introduction of several theories, apparently independent but later shown to be equivalent, there is now some consensus on a solution based on multi level selection. Inspired by biological evidence on altruistic acts among vampire bats, that were interpreted originally in the line of reciprocal altruism, we use agent-based simulation and propose an alternative explanation for their interpretation. We focus on the relationship between the parameter controlling the group size and the quantity of cheaters that the system is able to manage. In the present work, we show results obtained letting group size evolve under a fixed mutation rate, that continuously refill the population with egoist agents. Roosts split when they reach a critical size, which is subject to evolution too. This parameter is studied together with the mutation rate; the main result of the paper is the function relating (evolved) ideal group size and mutation rate in the range examined. We suggest an interpretation of this finding, along with a discussion of its generality.

Seasonal dispersal of pests: one surge or two?

M.D. Paulson, A.I. Houston, J.M. McNamara and R.J.H. Payne

Evolutionary theory is used to predict dispersal behaviour for species that exist within seasonal metapopulations (such as agricultural pests). Four sequential phases are found: no dispersal, dispersal from initially occupied patches, dispersal from later-colonised patches, and no dispersal. The third type of phase only occurs when reproductive rates are high, and we speculate that this may explain why, depending on the species of aphid, there can be either one or two surges of dispersal during a season. Other features of aphid biology are also explained, such as a summer crash in colony size. As season length increases, an additional surge of dispersal becomes more likely, which could have profound implications for pest management during future climatic warming.

Is life impossible?

J. Peck

Eigen's Paradox is a logical puzzle concerned with the origin of complex life. It is presumed that, early in the history of life, mutation rates were much higher than they are in contemporary organisms. According to Manfred Eigen, this implies that the maximum amount of information that could have been stably encoded in the genomes of early organisms must have been severely limited. In contemporary organisms, the mechanisms of error prevention and correction are quite complex. This leads to a 'chicken-and-egg problem'. How could life that is complex enough to allow the suppression of mutation to low levels have evolved while mutation rates were quite high? Eigen's calculations are based on the idea that, if the genome with the best-possible fitness can not be maintained in a population, then "The information ... would slowly seep away until it is entirely lost." However, this idea is not obviously based on any firm information theoretic foundation. What really matters is whether, in a stable population, organisms are able to generate phenotypes that are complex enough to allow for highly effective error prevention and correction mechanisms. Here, we re-analyze the problem using this phenotypic-complexity criterion. We find that there are conditions where much more information can be stably encoded in the genome than would follow from Eigen's criterion, despite the existence of relatively high mutation rates. We find that the highest levels of information content are obtained when recombination occurs, and when each possible phenotype is produced by many different genotypes.

Evolution of dominance and assortative mating under frequency-dependent disruptive selection

S. Peischl and K.A. Schneider

In models of frequency-dependent disruptive selection globally stable polymorphic equilibria with underdominance can occur. In the past, a number of possible mechanisms to reduce the inferiority of heterozygotes were studied. Such mechanisms include the evolution of dominance and the evolution of assortative mating. Usually, different evolutionary responses to negative frequency-dependent selection are treated as alternatives, and possible interactions are not very well understood. In contrast to previous studies, we focus on how assortative mating and dominance interact if one of them is evolving. In such models, four different components of selection interact with each other and can have direct and indirect effects. In this work we tease apart these components. We analyze a three-locus two-allele model, in which the primary locus has a major effect on a quantitative trait that is under a mixture of frequency-independent stabilizing selection, density-dependent selection and frequency-dependent selection caused by intraspecific competition for a continuum of resources. The second and third locus (modifier locus) determine the degree of dominance at the trait level and the strength of assortative mating, respectively. Our analysis shows that the interaction of dominance and assortative mating has a number of interesting effects. Especially when the strength of dominance or assortative mating is intermediate and the effects of modifier alleles are large.

When experimental psychology and behavioral ecology meet: Men perform worse than wasps

*J.-S. Pierre and P. Louapre**

We were interested in the human decision-making process considering the well-known dilemma exploration vs. exploitation in a foraging task. This dilemma can be found in a set of modern contexts like sport, gambling, information gathering or natural resource foraging. In behavioral ecology, this issue deals with the optimal foraging behavior framework and different optimal and proximal mechanisms were proposed to explain the patch leaving decision-making in predators, maximizing their fitness gain in a patchy resource. We tried to apply a process of decision-making proposed for parasitic wasps, to human subjects. Inspired by the neuroeconomics and experimental psychology, we used a computer game designed to approach such foraging strategy and cognitive process. Surprisingly, man seems to use a mechanism identical to the one proposed for parasitoids to reach the patch-leaving decision. This proximal mechanism converge with an optimal Bayesian model of the patch-leaving decision-making but humans appear less good than parasitoids and fails to adopt the optimal rule when faced to an even distribution of resources. These results can enlighten some aspects of the human decision-making process regarding to the Hominoids' life history.

Neuroeconomics in parasitoid. How to compute with a tiny brain?

J.-S. Pierre and P. Louapre

The literature on insect parasitoids often refers to a motivational model due to G. Waage as a heuristic for solving the patch leaving decision model: the forager enters a patch of hosts with an initial motivation to stay in the patch and go on foraging, which decreases linearly with time. Motivation suffers a sudden arousal when a host is encountered. This model was often compared to a Iwasa's et al Bayesian model, a theoretical way of reaching optimality in the patch problem which superficially exhibits a similar behaviour. The first one is a mechanistic process and the second a probability estimator. We show that the assumption of an exponential decay of motivation in the Waage's model is reasonable, and ensures a full convergence with Iwasa's et al model. Motivational processes would then be a case of emerging calculus, entering in the recent scientific field of neuroeconomics. A fully stochastic version of the model keeps also the convergence with Iwasa's bayesian estimator.

Lévy flights are better than optimal

M.D. Preston, J.W. Pitchford and A.J. Wood

'Optimal' behaviour in a biological system is not simply that which maximises a deterministic, or temporally and spatially averaged, fitness function. Rather, population dynamics and demographic and environmental stochasticity are fundamental evolutionary ingredients. Here we revisit the problem of optimal foraging, where some controversial recent studies claim organisms should forage according to so-called Lévy flights. We show that in an ecological scenario dominated by uncertainty and high mortality, Lévy flights can indeed be evolutionarily favourable. This is principally because the associated large variance and superdiffusive character at the population level, rather than a simple maximising of average encounter rate. These results have implications for stochastic search problems in general, and also to computational models of evolutionary optima.

Recruitment strategies and colony size in ants

R. Planqué

Ants use a great variety of recruitment methods to forage for food or find new nests, including tandem running, group recruitment and scent trails. It has been known for some time that there is a loose correlation across many taxa between species-specific mature colony size and recruitment method (Beckers *et al.* 1989). Until now, explanations for this correlation have focused on the ants' ecology, such as food resource distribution. However, many species have colonies with workforces that grow from a single queen over several orders of magnitude, and little is known about how a colony's organization, including recruitment methods, may change during growth. After all, recruitment involves interactions between ants, and hence the size of the colony itself may influence which recruitment method is used. Here we show using mathematical models that the observed correlation can also be explained by recognizing that failure rates in recruitment depend differently on colony size in various recruitment strategies. Our models predict that ant colonies should use only one recruitment method (and always the same one) rather than a mix of two or more. We also show that certain recruitment features, such as group size in group recruitment, in fact should not depend on colony size. These results highlight the importance of the organization of recruitment and how it affects, and is affected by, colony size. Hence these results should also expand our understanding of ant ecology.

Demography and the accumulation of culturally inherited skills: the origins of behavioral modernity

A. Powell, S. Shennan and M.G. Thomas

The Upper Palaeolithic Transition, sometimes referred to as the origin of behavioural modernity, is associated with the appearance of a package of increased symbolic and technological complexity. It occurred around 45,000 years ago in Europe and western Asia but somewhat later elsewhere in the old world. However, many of its features appear transiently some 45 to 25,000 years earlier in sub-Saharan Africa. Proposed explanations for this significant cultural shift include: biological / cognitive change, innovations in social structure and language, fluctuations in ecological / socio-economic conditions and the effects of population size increase on inter-group interaction / competition. However, none of these mechanisms adequately explain the spatiotemporal structuring of markers of behavioural modernity in the last 50,000 years or their earlier appearance in sub-Saharan Africa. We present a cultural learning simulation model that reflects key features of Pleistocene human demographic conditions. We show that the level of a cultural skill that can be maintained is related to the level of migratory activity amongst subpopulations but not to the number of subpopulations, when greater than 50. We also show that geographic heterogeneity in local subpopulation density or migratory range leads to stable spatial structuring of skill accumulation in contiguous space. Genetic estimates of population size change over time indicate that population densities in early Upper Palaeolithic Europe were similar to those in sub-Saharan Africa when the markers of behavioural modernity first appear. We conclude that demography is an important variable in explaining accumulation of loss of markers of behavioural modernity.

Evolution of individual genetic traits can reinforce group-level selection

S.T. Powers and R.A. Watson

It is well-known that the effectiveness of selection at the group-level depends on aspects of population structure, such as initial group size. It is nearly always assumed in models of group selection that such aspects of population structure remain fixed over evolutionary time, and, consequently, that the balance between individual- and group-level selection remains fixed. However, it is also well-known that individual traits can modify population structure, for example, organisms from bacteria to humans may be able to influence group size to some extent. Our contention is then that individual traits affecting population structure can evolve so as to influence the effectiveness of group-level selection, for example, by reducing preferred group size and hence increasing between-group variance because of sampling effects. We will present here a model of the concurrent evolution of group size preference and cooperative behaviour which demonstrates this process. Using this model we are able to show conditions under which a population can evolve from an initial state with only weak group-level selection and low levels of cooperation, to one where group-level selection is a highly effective force and cooperative behaviour dominates. We thus illustrate the potential for positive feedback between selection at the individual level and selection at the group level, in contrast to the standard view which holds that the former will always undermine the latter.

Is sexual conflict a consequence of parental effects on offspring fitness?

N.K. Priest

Darwin's prediction that traits that increase offspring production are favoured by natural selection does not seem to apply to the mating behaviour of the female fruit fly, *Drosophila melanogaster*. In this species, similar to many other sexual species, females are highly promiscuous – even though promiscuity reduces offspring production. We also know that male fruit flies express toxins in their seminal fluid that reduce the survival of their sexual partners. These findings have led to a number of challenges for the Darwinian paradigm. Why do males harm their mate? Why do females mate frequently despite male harm? And, does this mean we need a new model of evolution? The answers to these questions might be resolved by studies of parental effects, the consequences of parental condition and genotype on offspring phenotype. Here I present empirical studies of fruit flies and age-structured inclusive fitness theory which indicates that costs of frequent mating in the maternal generation are offset by fitness benefits seen in the offspring generation. I also present 2-locus, 2-generation population genetic theory which shows that parental genetic effects can alter the trajectory, rate and endpoint of phenotypic evolution. Each study indicates that parental effects may have a key role in the evolution of male harm of females.

A large population parental care game within a life history framework

D. Ramsey

In the 1970s Maynard Smith considered a game, in which parents decide whether to care for or desert their offspring. The number of surviving offspring depends simply on the parents' decisions. However, he was aware of the drawbacks involved in this model. For example, the expected gains from deserting depend on the strategies used within the population (the strategy profile). In order to model this feedback, parental care games should be modelled as games against the field. We consider such a model of a parental care game, in which there are no seasons. Males can be either searching for a mate or breeding. Females can be receptive, non-receptive or breeding. Two strategies are available to each individual: care or desert. The length of time spent in the breeding phase depends on the strategy used and the number of surviving offspring depends on the strategies adopted by both parents. Females move between the receptive and non-receptive states at fixed rates. The rate at which a searching male or receptive female finds a mate (and thus moves into the breeding state) is proportional to the fraction of the opposite sex looking for a mate. We derive the necessary conditions for a pure ESS to exist. We then consider the existence of stable polymorphic systems. It is shown that stable polymorphisms may exist in which *e.g.* all females care, but some males care and some desert. The framework presented can be extended to consider feedback between systems of mate choice and parental care.

Self-improvement for team-players: the effects of individual effort on public information

S.A. Rands

By putting effort into behaviors like foraging or scanning for predators, an animal can improve the correctness of its personal information about the environment. For animals living in groups, the individual can gain further information if it is able to assess public information about the environment from other group members. Earlier work has shown that consensus group decisions based upon the public information available within the group are more likely to be correct than decisions based upon personal information alone, given that each individual in a group has a fixed probability of being correct. This study develops a model where group members are able to improve their personal likelihood of making a correct decision by conducting some level of (costly) effort. I demonstrate that there is an evolutionarily stable level of effort for all the individuals within the group, if all group members benefit from an individual's effort. In smaller groups, optimal effort can either decrease or increase as group size increases, depending upon the costs incurred by the effort. These results have implications for how group-living animals should survey the environment, whenever the effort made affects the public information that an individual conveys to its fellow group members.

Rogers' paradox recast: Population structure and the evolution of social learning strategies

L. Rendell, L. Fogarty and K.N. Laland

While there has been considerable and recent theoretical analysis of the evolution of reliance on social learning, understanding of the relative effectiveness of different social learning strategies remains limited. We explored the evolution of reliance on social and asocial learning strategies using, for the first time, a spatially explicit stochastic model. We analysed the relative merits of four evolved strategies, two pure strategies (asocial and social learning) and two conditional strategies (the 'critical social learner', which learns asocially only when copying fails, and the 'conditional social learner', which copies only when asocial learning fails). We find that spatial structure generates outcomes that do not always conform to the finding of earlier theoretical analyses that social learning does not enhance average individual fitness at equilibrium (Rogers' paradox). While we describe circumstances under which the strategy of pure social learning increases the average fitness of individuals, we find that spatial structure introduces a new paradox, which is that social learning can spread even when it decreases the average fitness of individuals below that of asocial learners. We also show that the 'critical social learner' and 'conditional social learner' both provide solutions to the aforementioned paradoxes, although we find some conditions in which pure (random) social learning out-competes both conditional strategies.

Integrating metabolic and resource competition theories: simple modelling approaches

T. Revilla

The Metabolic Theory of Ecology (MTE) states that large scale patterns in communities and ecosystems (*e.g.* community structure, size distributions, biodiversity gradients) derive in great part from the relationship between individual metabolic rates with body mass and temperature. However, most of the conclusions of the MTE ignore or caricaturize the mechanisms of energy consumption, and ecological interactions. In this talk, by means of simple but realistic models, I will show how to introduce metabolic realism in resource competition models. As a consequence, key results from the MTE like the density-mass relationship and the energetic equivalence rule, are shown to be highly dependent on on the underlying physiological assumptions, such as allometries and stoichiometry. At the scale of communities, body mass scaling relationships depend on the dynamics of competition, spatial heterogeneity and the scale of body mass variation considered. Thus physiology, competition, and ecological stoichiometry can be major forces shaping community size distributions, and the MTE can be greatly improved by considering them.

Ants in a labyrinth

T.O. Richardson, K. Christensen, N.R. Franks, H.J. Jensen and A.B. Sendova-Franks.

Skewed activity distributions are ubiquitous within the social insects. Early non-spatial models have shown that such skewed divisions of labour can self-organise through the interaction of some task-related stimulus with differentially sensitive agents that perform work on the stimulus. We extend previous models by the inclusion of a stimulus 'landscape' with mobile agents that move through it and modify its structure as they perform work. The inclusion of a spatial dimension induces a 'percolation' effect which means that a small change in the sensitivity of an agent can cause a large change in the probability of it performing some work. This effect is akin to phase-transition phenomena in many physical and chemical systems. We emphasise that the extension of classic fixed-threshold models of division of labour to include space means that they can now be treated as a special case of diffusion in disordered media - a well studied branch of statistical mechanics.

How a simple threshold-rule accounts for sophisticated ant decision-making

E.J.H. Robinson, J.A.R. Marshall and N.R. Franks

Ant colonies choose the best new nest by making collective decisions built on the behaviour of individual scouts. Previous work proposed a choice mechanism involving quality-dependent recruitment latencies and direct comparisons of available nests by individual ants (Mallon *et al.* 2001). More recent experimental work (Robinson *et al.* 2009) proposes that recruitment latency and nest comparison can be explained as side-effects of a simple rule in which ants compare the quality of a nest only to an internal threshold of acceptability, and respond either by accepting the nest, or by rejecting it and searching for alternatives. This threshold hypothesis forms a simple yet sophisticated mechanism for collective decisions, without requiring the ants to remember nest quality. We used a Monte-Carlo model of threshold-based decision-making to demonstrate that this mechanism can account for apparent comparison and quality-dependent latencies in a range of nest choice contexts. We make testable predictions to distinguish between the two proposed mechanisms of collective choice. We also investigate the effects of variation in acceptance threshold between individuals (the colony threshold distribution) on the collective decision. We show that colony-level comparison and choice can emerge, without direct comparison by individuals.

A simple generalisation of neutral biodiversity theory resolves many of its problems

J. Rosindell

We present a generalisation of Hubbell's Unified Neutral Theory of Biodiversity and Biogeography. The original neutral model has demonstrated its ability to reproduce many widespread ecological patterns such as species abundance distributions and species area curves, but it has mostly failed to combine this with convincing timescales for the turnover of species amongst other things. Our new model is simple enough to remain tractable, both analytically and computationally. We show that it resolves several timescale related problems without sacrificing any of the existing achievements of the original model. Neutral theory can thus be defended against many long-standing criticisms, but some of the parameters present in the existing neutral model will now require reinterpretation.

Herbivores enable plant survival under nutrient limited conditions in a model grazing system

S.C. Ryrie and I.C. Prentice

The action of herbivores in removing plant tissue may at first sight appear to be detrimental to the plants upon which they are grazing. However, this traditional view is now being questioned by studies which suggest that plants can benefit from grazing through a number of different mechanisms. In this paper we have studied the effects of nitrogen cycling on this interaction between plants and herbivores. This investigation was inspired by discussions of the grazing optimisation hypothesis of McNaughton (Am. Nat. 113, 1979). We investigate a simple model of a grazing system which has five compartments, and with no *a priori* assumptions about whether the system might be subject to top-down or bottom-up control. By adopting piecewise linear approximations to the nonlinear functions which describe the rate of uptake of nutrients by plants, and the rate of consumption by herbivores, it is possible to make an analytical study of the equilibrium states, and of their stability. We find that at equilibrium in this model, and under certain nutrient limited conditions, the presence of herbivores is not only beneficial to plant growth but can be essential to plant survival. Plants are able to survive in the presence of herbivores under conditions in which they would not be able to survive alone. It is also possible to identify values of certain parameters of the model which are in some sense 'optimal' for both plants and herbivores, though this has not been linked to an evolutionary development of the parameters.

Romantic memories: Duration of courtship effort when participants have a finite memory

R.M. Seymour and P.D. Sozou

We consider a male and a female in a courtship encounter over continuous time. Both parties pay participation costs per unit time. The game ends when either one or other of the parties quits or the female accepts the male as a mate. We assume that there is a binary variable which determines whether the male is a 'good' or 'bad' type from the female's point of view, according to either his condition or his willingness to care for the young after mating. This variable is not directly observable by the female, but has fitness consequences for her: she gets a positive fitness payoff from mating with a 'good' male but a negative fitness payoff from mating with a 'bad' male. We have recently shown that, if the participants have no memory, there are evolutionarily stable equilibria with extended courtship: a 'good' male will wait indefinitely for the female to mate; a 'bad' male has a finite probability per unit time of quitting; and a female has a finite probability per unit time of ending the game by agreeing to mate (Journal of Theoretical Biology 256, 1-13, 2009). In the present study, we consider a situation in which both the male and female have a perfect memory of finite length. We show that an extended courtship equilibrium is still possible providing the memory does not exceed a critical length, but that no such equilibria are possible if the memory is too long.

Reproducing networks

R. Southwell and C. Cannings

Large networks of interacting organisms are abundant in nature. Two effects make these networks very dynamic, birth (successful organisms reproduce) and death (unfit organisms die). Although simple factors often dictate when organisms reproduce or die, complex networks, with emergent properties, frequently appear. We model organisms as vertices in a network, employing strategies according to their type. The idea is that vertices reproduce (generating offspring with the same neighbourhood and strategy), whilst vertices that perform poorly (in games with their neighbours) get destroyed. Our deterministic models can produce a myriad of different dynamics- ranging from the very simple to the very complex. Under some games networks' development can be completely understood. Other games can generate complex behaviour including chaotic growth patterns or self replication. Sometimes small initial structures grow and fragment, leading to vast 'ecosystems' containing thousands of different connected structures which grow, change and self replicate. It is pleasing that our microscopic 'survival of the fittest' growth model can produce one of the most important macroscopic features of life - self replication. We will introduce this model and a variety of others where the neighbourhood of the offspring depends upon its parent's in different ways. These could be applied to situations in biology, social sciences and economics. We will discuss how mathematical techniques can sometimes be applied to simplify the dynamics. We will give examples of complex self replicative processes that can occur, and we will discuss how self replication often persists in presence of added stochasticity.

An evolutionary basis for social discounting

P.D. Sozou

Social discounting in economics involves applying a diminishing weight to community-wide benefits or costs into the future. It impacts on public policy decisions involving future positive or negative effects, but there is no consensus on the correct basis for determining the social discount rate. This study presents an evolutionary biological framework for social discounting. How an organism should value future benefits to its local community is governed by the extent to which members of the community in the future are likely to be its kin. Trade-offs between immediate and delayed benefits to an individual or to its community are analysed for a modelled patch-structured iteroparous population with limited dispersal. The (constant) population is governed by a Moran-type dynamic process in which there are separate hazard rates for (i) individuals and (ii) entire patches to be replicated or killed. It is shown that the social discount rate is generally lower than the individual (private) discount rate. The difference in the two rates is most pronounced, in ratio terms, when the dispersal level is low and the hazard rate for patch destruction is much smaller than the individual mortality rate. When decisions involve enforced collective action rather than individuals acting independently, social investment increases but the social discount rate remains the same.

Offspring provisioning in the pinnipeds: insights from an annual routine model

P.A. Stephens, A.I. Houston, K.C. Harding, I.L. Boyd and J.M. McNamara

In spite of a high degree of morphological similarity, species of pinniped (seals and their allies) display striking differences in their offspring provisioning behaviour. At one extreme are fasting strategies, in which females remain with their pup for several days or weeks from birth until the pup is weaned, relying entirely on stored energetic capital. At the other extreme are foraging cycle strategies, in which pups are left ashore for prolonged periods whilst the female forages. Foraging bouts are interspersed with periods of suckling ashore and pups may not be weaned for many months. These strategies are broadly equivalent to the concepts of capital and income breeding. Previous assessments of the adaptive value of different offspring provisioning strategies have emphasized the role of body mass but certain well-studied examples confound attempts to attribute variation directly to body mass alone. We used dynamic programming to examine the role of food supply in shaping the offspring provisioning strategies of female pinnipeds. We also assessed the importance of two poorly-documented aspects of pinniped biology: the costs of carrying fat stores and the relative independence of growing pups. Of the variables that we assessed, pup development to independence was of overwhelming importance in dictating maternal strategies. This suggests important hypotheses for further research on the evolution of pup provisioning in pinnipeds and, more generally, for the adaptive value of capital and income breeding strategies.

The evolution of teaching

P. Strimling, L. Fogarty and K.N. Laland*

Teaching behaviour, whereby an individual actively imparts information to a naïve conspecific, has been shown in a diverse range of animals including ants, meerkats and pied babblers. This taxonomic distribution suggests that teaching has evolved several times independently. We develop the first mathematical model to investigate the evolution of teaching and find that it is highly dependent on the value of information taught, the average relatedness between a focal individual and their teacher or cultural role model, and the level of information in the population in general. We also show that the presence of teachers in the population increases the fitness of both teachers and non-teachers suggesting that teaching benefits the population at large. Finally we discuss the predictive power of the model and show that it can be used with data gathered in the field.

How much sperm should an attractive male invest?

S. Tazzyman and A. Pomiankowski

Sperm competition theory has focussed on the evolution of ejaculate expenditure strategies across different species, populations, or discrete mating roles characterised by different levels of sperm competition. Few studies have considered the extent to which male ejaculate expenditure is influenced by continuous change in male phenotype within a population. Here, we model how optimal ejaculate expenditure responds to two sources of continuous variation: the quantity of resources allocated by a male to mating within a breeding season, and the resource cost of obtaining a mate. We find that when males vary in the amount of resources available for reproduction, all males are selected to use the same ejaculate expenditure strategy. However, when males vary in the cost of obtaining a mate, males with a lower cost will be selected to invest fewer sperm per mating than males whose cost is higher. These results provide a novel insight into the evolution of male ejaculate expenditure strategies, showing that individual constraints on the ability to secure matings can lead to variation in ejaculate expenditure even when the risk of sperm competition is the same for all males.

Decision accuracy and the evolution of ecological specialisation

C.R. Tosh, D.W. Franks, J. Krause and G.D. Ruxton

The idea that increased resource-related decision accuracy can promote the evolution of ecological specialisation is gaining support from empirical studies. We present one of the first theoretical treatments of this idea. We model the consumer-resource interaction as a neural network receiving shape information from a range of artificial resources. We use an evolutionary algorithm to train the networks to be generalists or specialists under different regimes of punishment/reward for accepting non-host resources, and then observe their decision accuracy during a standardised task. Somewhat counter-intuitively, but entirely consistent with observations in nature, specialists make more accurate decisions than generalists when acceptance of non-host resources makes a slightly positive contribution to fitness. Generalists outperform specialists when acceptance of non-host resources makes a negative contribution to fitness. The obvious analogy between some gross phenomena within our model predictions and learning processes in humans (*e.g.* learning through encouragement) made us wonder if we could replicate our results through analysis of short term learning processes in humans. We present an interactive computer game with which we are exploring this possibility.

On the generality of stability-complexity relationships in Lotka-Volterra ecosystems

S.E. Townsend, D.T. Haydon and L. Matthews

This work contributes to the stability-complexity debate using permanence and local stability as definitions of stability. While local stability has made a major contribution to the debate over the last few decades, permanence is widely considered to be a more satisfactory definition of ecosystem persistence and has relatively recently become available as a tool for assessing the global stability of Lotka - Volterra communities. Here, we relate Lotka-Volterra food web complexity to permanence and local stability, and correlate local and global stability. We document positive relationships between permanence and complexity and a positive correlation between the probability of local and global stability. We investigate further the frequency of discrepancy (attributed to fragile systems that are locally stable but not permanent or locally unstable systems that are permanent and have cyclic or chaotic dynamics) and the causes of non-permanence at the boundary of the state-space. A key finding is that locally stable interior equilibria tend to have all locally unstable boundary equilibria. Since a stable boundary is inconsistent with permanent dynamics, this can explain the observed positive correlation between local interior stability and permanence. Our findings suggest that at least in Lotka-Volterra systems, local stability may be a better measure of persistence than previously thought.

Periodic host absence and the evolution of plant pathogens

F. van den Berg, N. Bacaer, J.A.J. Metz, C. Lannou and F. van den Bosch

Many natural and agricultural ecosystems are characterised by periodic host absence. These periods of host absence are often relatively large and are known to have profound effects on the dynamics of parasite populations. However, little is known about the selection pressures such seasonality might impose on a parasite's life-cycle characteristics. This presentation aims to give an overview of theoretical and experimental approaches presently undertaken in a BBSRC-INRA collaboration towards understanding the effect of periodic host absence on the evolution of pathogen life cycle characteristics. In this presentation it is shown that a period of host absence does put a strong selection pressure on the pathogen and that whether a longer period of host absence selects for lower or higher transmission rates depends on the type of trade-off that the pathogen faces. Key finding are: 1. A trade-off between the pathogen's transmission rate in the presence of the host and its survival in the absence of the host in combination with a model for discontinuous host growth can, surprisingly, not explain the coexistence of two genetically distinct phenotypes of take-all of wheat. 2. Increased periods of host absence seem to select for lower transmission rates when the pathogen faces a trade-off between within season transmission and between season survival, and higher transmission rates when the pathogen faces a trade-off between within season transmission and disease induced host death. 3. The length of the period of host absence is a key determinant of a pathogen's transmission rate.

Evolutionary dynamics of foraging strategies in ants: interference competition promotes diversity

L. van Oudenhove, X. Cerdá and C. Bernstein

Ants use species-specific foraging strategies, either searching for food individually or collectively, by recruiting other workers. What are the evolutionary and ecological conditions that make possible the sympatric coexistence of these strategies at the community level? We analyse the consequences of the foraging strategies for the evolutionary dynamics of foraging traits by means of mathematical modelling. The model links processes operating at a microscopic scale (interactions between foraging ants), to that of macroscopic evolution through a stochastic mutation-selection processes based on the phenotype of individuals, defined as the ants' colony. Evolutionary change occurs in a trait involved in the foraging process. The assumption is that collective foraging behaviour enhances both competitive and foraging ability, but depends on mild environmental conditions. A general, deterministic, model predicts that: i) In populations exclusively subjected to exploitative competition, the optimal strategy is either to forage individually or collectively depending on the environmental conditions but the coexistence of both strategies is precluded. ii) In populations submitted to both exploitative and interference competition, it exists conditions that lead to the emergence and coexistence of both collective and individual foraging strategies. A more explicit model is proposed in order to extend the former predictions to a more complex and biologically realistic scenario: stochastic simulations illustrate the emergence of polymorphism in the foraging strategies at a community level.

Does choice take time?

M. Vasconcelos, J. Aw, T. Monteiro and A. Kacelnik

The Sequential Choice Model (SCM) assumes that animals are mostly adapted to encounter opportunities sequentially, and that prey differ in value according to how they contrast with background opportunities. According to SCM, upon meeting a potential target, a value-dependent process builds up until a pursuing response is triggered. Triggering occurs, on average, faster for high value than low-value prey, and the latency to respond reflects the probability that the opportunity will be passed over. When more than one target is faced simultaneously, each elicits its own build-up process, and the one which triggers earlier is pursued. This leads to two predictions. First, proportion of choices in simultaneous encounters should be predictable from the distribution of latencies in sequential encounters. Second, latencies in simultaneous encounters should be shorter than in sequential ones, as the build-up processes for different options cross-censor one another. This shortening of latencies should be greater for the item with lower value and longer latencies, as its distribution of latencies will be censored more severely. Contrary to alternative putative mechanisms of choice, choice does not involve a time-consuming deliberation. We offer new evidence supporting this model using a variety of procedures, including risky choice, comparative valuation and multi-alternative scenarios, wherein European starlings (*Sturnus vulgaris*) encounter food sources either alone or simultaneously.

Conflict between sexual selection signals and species recognition

T. Veen and S. van Doorn

Many species use mating signals to discriminate between partners of different quality. The same mating signals often also serve a function in species recognition in areas of secondary contact between closely related species. As a result of this dual use of signals, individuals may have to compromise the opportunity to select a mate of high genetic quality, in order to avoid the costs associated with hybridization. Indeed, conflict between intraspecific mate choice and species recognition occurs frequently in nature, and various solutions to lessen the conflict seem to have evolved. Nonetheless, the potential evolutionary consequences of the conflict between good-genes sexual selection and species recognition are not fully understood. For that reason we used individual-based simulations to model mate choice and species recognition in a hybrid zone along an environmental gradient. When only one signal is involved, the conflict might be resolved by one species giving up the good-genes benefit altogether, or by different levels of investment in preference and signal expression in the two species. For multiple signals, a mix of these and good-gene equilibria is found, depending on the cost of hybridization and the amount of information that the signals provide about genetic quality. Our model shows the importance of single versus multiple signals for resolving the signaling conflict. Furthermore it reveals solutions that may help reveal subtle species recognition mechanisms in nature or explain counter intuitive mate choice patterns, such as the preference for heterospecific calls in tropical frogs.

The propagation of social information in primate groups

B. Voelkl

Primates are known for their ability to learn new behaviours socially and to develop temporally stable behavioural traditions. The social structure of primate groups is highly diverse and it has been proposed that differences in the group structure influence the patterns of information propagation. However, because most formal transmission models usually ignored the social dynamics of multi-agent societies this proposition has not been tested so far. Here we provide results of a simulation study of information propagation on social networks of 70 primate groups comprising 30 different species. We found that models that include the social structure of a group differ significantly from those that assume random associations of individuals. Overall information spreads slower in the structured groups than in the well mixed scenario. While we found only a minor effect on the path lengths of the transmission chains, robustness against forgetting was strongly influenced by the group structure. Interestingly robustness against forgetting was not correlated with propagation speed but could be predicted reasonably well by relative strength assortativity a structural network metric. Our results show that incorporating group structure in any social propagation model significantly alters its predictions for spreading patterns, speed and robustness of information.

Fundamental insights into the random movement of animals from a single distance-related statistic

D. Waxman

Statistical theories of animal movement have often been based on models of random walks where movements take place in discrete steps and occur at discrete times. The multiplicity of distributions required in these approaches to describe animal movement (*i.e.* the distributions of angles, discrete steps, and times), have effects that cannot be simply disentangled, and hence cannot be unambiguously determined. Here we present a mathematical formulation of continuous animal movements. In this new framework, it is shown that a single time-dependent distance statistic, the mean square displacement, which may be directly measured or mathematically modelled, is a central determinant of such random walks and encapsulates key information about the statistical properties of animal movements. The model and methodology presented here not only allow the determination of what were previously viewed as independent aspects of animal movements, such as the distribution of angular changes in direction, but also, because of the new emphasis on the mean square displacement, may open up a new set of questions concerning animal movement and related phenomena. The results established in this work are directly applied to the foraging behaviour of Pharaoh's ants and very close agreement is found between observation and theory.

The origin of species by natural and sexual selection

F.J. Weissing

Speciation – the origin of new species – is the source of the diversity of life. A theory of speciation is essential in order to link poorly understood macro-evolutionary processes (like adaptive radiations) to rather well understood micro-evolutionary processes (like natural selection). Recently, theoreticians have claimed that, in contrast to earlier theories, speciation is 'adaptive', *i.e.* fully driven by natural or sexual selection. I will critically review these claims and point out some important gaps and shortcomings of the underlying models. Adaptive speciation under the sole action of either disruptive natural selection or disruptive sexual selection is a theoretical possibility, but it only occurs under highly restrictive conditions or under rather unrealistic assumptions. This does not necessarily imply that adaptive speciation is unlikely. By means of models including both natural and sexual selection, I will demonstrate that the interplay of both forms of selection can induce adaptive speciation under quite natural and broadly applicable conditions.

Index