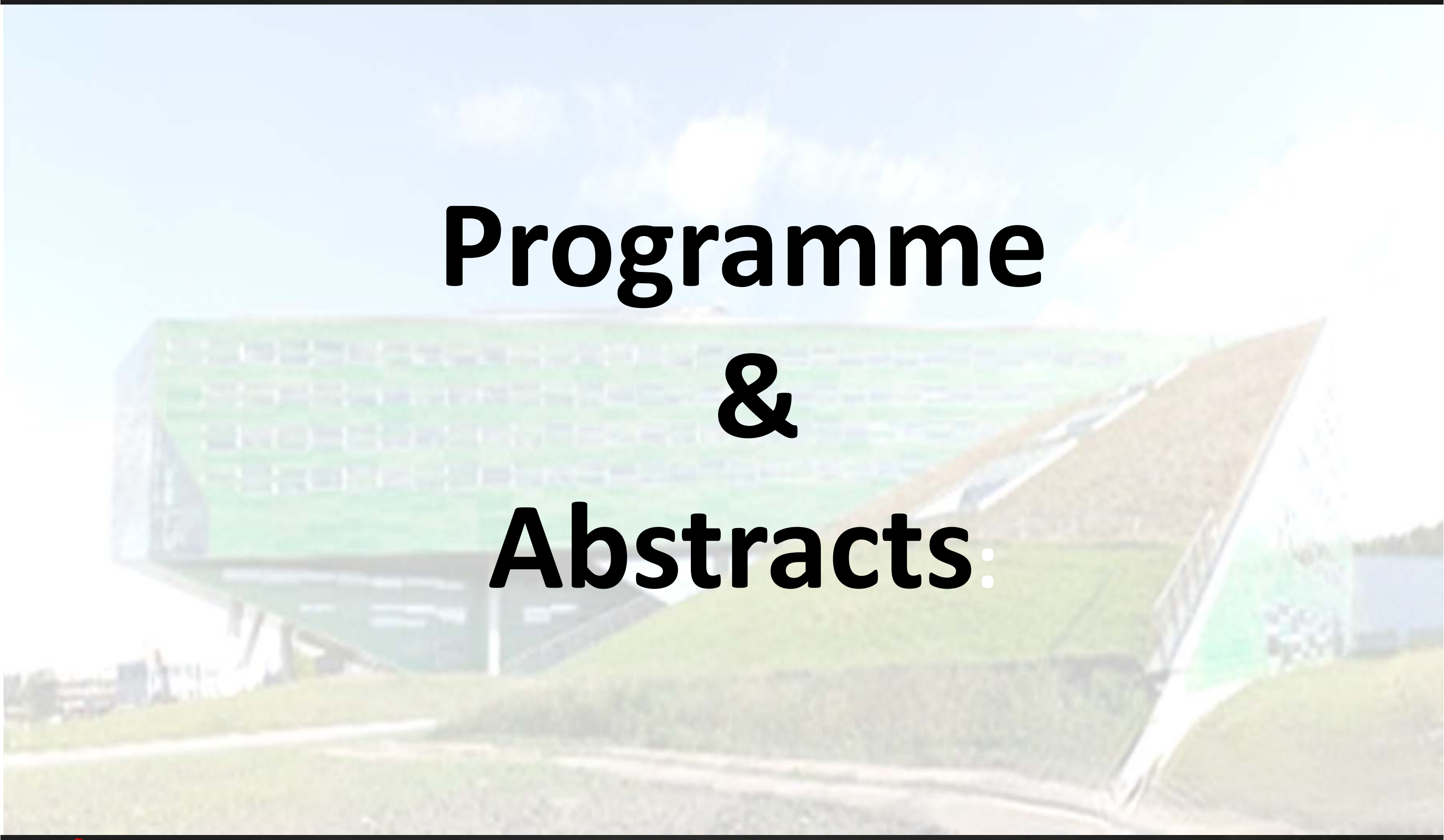
MATHEMATICAL MODELS IN ECOLOGY AND EVOLUTION



Programme & Abstracts:

university of groningen

www.mmee2011.evobio.eu
mmee2011@rug.nl

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Rampal Etienne
Bob Planque
Sander van Doorn
Franjo Weissing

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Wednesday 17th August 2011			
	5161.0151	5161.0105	5161.0253
16.00	*Start registration (CvL central hall)*		
17.30	*Buffet & registration (CvL central hall)*		
19.00	*Public lecture (5161.0151)* Simon Levin - Evolutionary perspectives on public goods and collective behaviour		

Thursday 18th August 2011			
	5161.0151	**5161.0105**	**5161.0253**
08.30	*Registration (5161.0151)*		
08.50	*Conference welcome (5161.0151)*		
09.00	*Plenary (5161.0151)* **Paulien Hogeweg – Evolution of evolvability - Structuring of genomes, network and ecosystems**		
10.00	*Coffee*		
	Pattern formation I	**Life history**	**Species interactions**
10.20	Kirsten ten Tusscher – *In-silico* evolution of developmental networks	Pete Trimmer – The ecological rationality of state-dependent valuation	Carlos Melian – Eco-evolutionary dynamics in super-networks
10.45	Charlotte Hemelrijk – Some causes of the variable shape of flocks of birds	Andrew Higginson – Effects of costs of energy reserves on body size and adiposity	Francisco Encinas Viso – Phenology drives mutualistic network structure and diversity
11.10	Daan Reid – Modelling the hydrodynamics of infinite schools of fish	John Bryden – Can it be worth delaying reproduction in a steady environment?	Aniek Ivens – The co-evolution between mutualism and condition-dependent migration
11.35	*Plenary (5161.0151)* **Homayoun Bagheri – How can we understand ancient evolutionary transitions such as multicellularity and cellular differentiation?**		
12.20	*Lunch & Posters*		
13.40	*Plenary (5161.0151)* **Chris Klausmeier – Theoretical approaches to plankton ecology**		
	Pattern formation II	**Learning & culture**	**Pathogens I**
14.40	Johan van de Koppel – Diatom-sedimentation feedback generates a self-organised landscape	Luke McNally – Cooperation and the evolution of intelligence	Cornelis Drost – Epidemiology of overtreatment in vector-borne diseases
15.05	Jasper Ruifrok – The role of herbivores as ecosystem engineers	Daniel Jones – Social learning and evolution in a structured environment	Femke van den Berg – The evolutionary ecology of plant pathogens
15.30	Jon Yearsley – Fireox: an SIR model to describe the spread of smouldering peatland fire	Hannah Lewis – Transmission fidelity is the key to the build-up of complex culture in humans	Marek Kwiatkowski – Modelling the ecology of symbiont-mediated protection against parasites
15.55	*Coffee*		
16.25	*Plenary (5161.0151)* **Corina Tarnita – Limitations of inclusive fitness theory**		
	Social evolution	**Environmental change**	**Population genetics**
17.15	James Marshall – The generality of inclusive fitness theory	Marjolein Lof – Optimal timing of reproduction in a warming world	Dan Cohen – A general model of genetic diversification by correlated pleiotropic interactions
17.40	Peter Sozou – Asymmetric helping and harming behaviour	Nicolas Alcala – Genetic diversity of metapopulation under temporal changes of connectivity	Carina Mugal – Evolutionary dynamics of dN/dS
18.05	Sander van Doorn – The evolution of generalized reciprocity on social interaction networks	Mario Pineda-Krch – Evolutionary diversification under seasonally varying reproduction	Harold de Vladar – Ensembles of evolutionary histories: adaptation, simulations and inference
19.30	*Conference dinner*		

Friday 19th August 2011			
	5161.0151	**5161.0105**	**5161.0253**
09.00	*plenary (5161.0151)* **Sally Otto – Inferring the past for traits that alter speciation and extinction**		
10.00	*Coffee*		
	Community ecology	**Communication I**	**Foraging strategies**
10.20	Rampal Etienne – Making inferences on diversification from molecular phylogenies	Mark Broom – Some mistakes go unpunished: the evolution of “all or nothing” signalling	Zoe Cook – The effects of recruitment strategy on the benefits of polydomy in ant colonies
10.45	Stephen Cornell – Analytical properties of species area curves in spatial neutral models	Lev Yampolsky - To own or to own not: A game theory model of resource ownership and defence	Andrea Kölzsch – Empirical evidence for Lévy signatures in mud snail movement
11.10	David Alonso – Stochastic metacommunity theory	Sam Tazzyman – Fixed and dilutable benefits: female choice for good genes or fertility	Monique de Jager – Mussels on the move: How Levy walks evolved in a self-organizing system
11.35	Omar Al Hammal – Power testing of neutral theory	David Ramsey – A model of single-sided mate choice based on multiple traits	Axel Rossberg - Biodiversity and dietary diversity in marine food webs
12.00	*Lunch & posters*		
13.30	*plenary (5161.0151)* **Hans Metz – The geometry of meso-evolution**		
	Ecological niches	**Communication II**	**Predator-prey**
14.30	Géza Meszéna – Mathematical niche theory	Bob Planqué – Maintenance of bird song dialect borders	Steve Alpern – Ambush vs cruise search by a predator looking for its prey
14.55	Xiaoguang Du – A niche-based mechanism for neutral-like patterns	Matthias Franz – Multiple niches for agonistic behaviours can emerge from dyadic relationship	Robert Arculus – A version of the predator-prey search game where the predator is silent
15.20	Daniel van der Post – Evolution of cooperative foraging: self-organization and patch depletion	Franjo Weissing – The evolution of individual variation in communication strategies	Ellen van Velzen – The evolution and coexistence of herbivores under between-plant competition
15.45	*Coffee*		
16.15	*plenary (5161.0151)* **Andreas Wagner – The origins of evolutionary innovations**		
	Pathogens II	**Miscellaneous I**	**Miscellaneous II**
17.15	Meghan Fitzgerald – The effects of ecology on a web-stealing spider	Tim Fawcett – Equation overload: what deters empirical biologists from citing theoretical work?	Joost van de Heuvel – The predictive adaptive response: a life history model of *Bicyclus anynana*
17.40	Loïc Chaumont – On emergence times of competition processes	Krysztof Argasinski – In which currency are paid payoffs in evolutionary games?	Somdatta Sinha – Population dynamic consequences of interactions among life stages of insects
18.05	Romain Bourget – Competition processes, a tool to model pathogen adaptation time	Ivan Puga-Gonzalez – Emergence of coalitions, their reciprocation and their exchange in a model	Atiyo Ghosh – Quantifying introgression risks in random environments with hazard rates
18.30	*Presentation of awards & conference close (5161.0151)*		

Mathematical Models in Ecology and Evolution 2011

MMEE 2011

University of Groningen

17 – 19 August 2011

Programme & Abstracts

CONTENTS

KEYNOTE LECTURES

EVOLUTIONARY PERSPECTIVES ON PUBLIC GOODS AND COLLECTIVE BEHAVIOUR

Simon Levin
Princeton University, USA

Ecological and economic systems are alike in that individual agents compete for limited resources, evolve their behaviors in response to interactions with others, and form exploitative as well as cooperative interactions as a result. In these *complex adaptive systems*, macroscopic properties like the flow patterns of resources like nutrients and capital emerge from large numbers of microscopic interactions, and feed back to affect individual behaviors. Contagion can lead to critical transitions from one basin of attraction to another, as for example with eutrophication, desertification, pest outbreaks, and market collapses. In both sorts of systems, evolution of one type or another leads to the differentiation of roles and the emergence of system organization, but with no guarantee of robustness. It is crucial to understand how evolutionary forces have shaped individual behaviors in the face of uncertainty. In this talk, I will explore the common features of these systems, especially as they involve the evolution of intragenerational and intergenerational resource allocation. In particular, I will focus on the evolution of cooperation in dealing with public goods, common pool resources and collective behavior. Human and non-human groups alike exhibit prosocial behavior, acting in ways that benefit others. I will describe work in progress with Avinash Dixit and others exploring the consequences of prosociality for the decisions individuals make in public goods situations, apply these and related theoretical approaches to cooperative grazing of cattle and to management of small fisheries, and ask why prosociality exists.

EVOLUTION OF EVOLVABILITY - STRUCTURING OF GENOMES, NETWORKS AND ECOSYSTEMS

Paulien Hogeweg
University of Utrecht, the Netherlands

Evolution of evolvability has been a contentious issue in evolutionary theory because evolvability does not give immediate benefits. Here we show in computational models that through structuring of genomes, regulatory networks and ecosystems long term information integration does take place, and leads to evolution of evolvability. Moreover we show that some surprising recent observations are readily explained as generic properties of such multilevel evolutionary processes. For example (1) the fast adaptation of yeast to new environments which involves only few fixed mutation but large changes in the transcriptome as seen in experimental evolution; and (2) the relative large genomes of early common ancestors and the prominent role of gene loss in subsequent species radiation and adaptation as seen in phylogenetic reconstructions, emerge in such models as side-effects.

HOW CAN WE UNDERSTAND ANCIENT EVOLUTIONARY TRANSITIONS SUCH AS MULTICELLULARITY AND CELLULAR DIFFERENTIATION?

Homayoun Bagheri
University of Zürich, Switzerland

All complex life forms that grow beyond microscopic scales are multicellular. Multicellularity and differentiation are fundamental organizational themes in development, and have played a key role in the evolution of life. How does one study the deep evolutionary transitions that led to these traits? In this talk, I use bacteria as a case study to understand the origins of multicellularity in simple life forms. I summarize results from phylogenetic reconstruction and genome comparisons, theoretical models of population dynamics, strain isolation, and laboratory experiments that shed light on different aspects of the evolution of multicellularity and cellular differentiation.

THEORETICAL APPROACHES TO PLANKTON ECOLOGY

Chris Klausmeier
Michigan State University, USA

Phytoplankton are globally important organisms, responsible for up to 50% of the world's primary production. They also make an ideal model system for developing and testing ecological theory. In this talk I will discuss three patterns found in phytoplankton communities: 1) Spatial patterns: the vertical distribution of phytoplankton in poorly-mixed water columns using reaction-diffusion equations; 2) Temporal patterns: the seasonal succession of species using forced differential equations and hybrid dynamical systems; 3) Community patterns: assembling communities using methods from evolutionary game theory.

LIMITATIONS OF INCLUSIVE FITNESS THEORY

Corina Tarnita
Harvard University, USA

For the past four decades kin selection theory, based on the concept of inclusive fitness, has been a major theoretical attempt to explain the evolution of altruism and of social behaviour. I will compare this approach to methods from evolutionary game theory and population genetics. I will discuss the applicability and the limitations of inclusive fitness and show that it requires assumptions that are restrictive and unlikely to hold for any realistic situation. I will argue that standard natural selection theory in the context of precise models of population structure represents a simpler, more solid and more general approach.

INFERRING THE PAST FOR TRAITS THAT ALTER SPECIATION AND EXTINCTION

Sally Otto
University of British Columbia, Canada

I will describe BiSSE, a likelihood-based approach to infer how speciation and extinction rates depend on the state of a particular character. The phylogenetic tree of a group of species contains information about character transitions and about diversification: higher speciation rates, for example, give rise to shorter branch lengths. The likelihood method that we have developed uses the information contained in a phylogeny and integrates over all possible evolutionary histories to infer the speciation and extinction rates for species with different character states. Our method can be used to provide more detailed information than previous methods, allowing us to disentangle whether a particular character state is rare because species in that state are prone to extinction, are unlikely to speciate, or tend to move out of that state faster than they move in.

THE ORIGINS OF EVOLUTIONARY INNOVATIONS

Andreas Wagner
Institute of Evolutionary Biology and Environmental Studies, Switzerland

Life can be viewed as a four billion year long history of innovations. These innovations range from dramatic macroscopic innovations like the evolution of wings or eyes, to a myriad molecular changes that form the basis of macroscopic innovations. We know many examples of innovations -- qualitatively new phenotypes that can provide a critical advantage in the right environment -- but have no systematic understanding of the principles that allow organisms to innovate. Most phenotypic innovations result from changes in three classes of systems: metabolic networks, regulatory circuits, and protein or RNA molecules. I will discuss evidence that these classes of systems share two important features that are essential for their ability to innovate.

THE GEOMETRY OF MESO-EVOLUTION

Hans Metz
University Leiden, the Netherlands

Adaptive dynamics (AD) is a recently developed framework geared towards making the transition from micro-evolution to long-term evolution based on a time scale separation approximation. This separation allows defining the fitness of a mutant as the rate constant of initial exponential growth of the mutant population in the environment created by the resident community dynamics. This definition makes that resident types have fitness zero. If in addition it is assumed that mutational steps are small, evolution can be visualized as an uphill walk on a fitness landscape that keeps changing as a result of the evolution it engenders. AD arguments are largely local in character. Hence they can only deal with what might be called meso-evolution. For longer timescales (macro-evolution) it becomes necessary to look at general developmental and morphological (*sensu lato*) arguments that bear on the larger scale geometry of fitness landscapes. From this enlarged perspective the low dimensional fitness landscapes studied in AD can be seen as the surfaces at the top of ridges in a much higher dimensional landscape over potential morphologies, with the abyss around the ridges created by the lack of a proper development or functioning. The location of the ridges and abysses is grossly the same for large sets of possible environmental conditions. Biologists express this constancy by referring to the corresponding selective processes as internal. High dimension and ridgyness can conspire in a various ways. For example, developmental systems leading to mutation distributions that are in some way aligned with the ridges evolve much faster than systems where such is not the case, and mutational steps far more often than not make its bearer land in the fitness abyss, and only the small steps keep it on the top. The latter observations provide a theoretical justification for the assumptions made in AD.

CONTRIBUTED TALKS

GENETIC DIVERSITY OF METAPOPULATION UNDER TEMPORAL CHANGES OF CONNECTIVITY

Nicolas Alcala & S. Vuilleumier
Department of Ecology and Evolution, Switzerland

Genetic diversity is essential for population survival and adaptation to changing environments. The pattern of population genetic diversity is known to be affected by various aspects of its spatial structure, but the structure is often considered constant through time. However, during the millions years of a species' life-time, events of connection and disconnection of populations occur both occasionally and cyclically. Glaciations, reduction or rise of sea levels generated alternately isolated and fused habitats, shaping nowadays species diversity. Similarly, recent anthropogenic changes like urbanization and agriculture or global warming are modifying connectivity patterns of populations. How abrupt and cyclic changes in connectivity affect the genetic signature of populations has been poorly explored yet and is the object of our study. Given various migration rates, mutation rates, degrees of fragmentation and populations sizes, we document analytically the impact of temporal change in connectivity on genetic diversity. We observe that the frequency and duration of connection and disconnection events and the degree of fragmentation (number of populations) have a non-monotonous effect on genetic diversity. We demonstrate that temporal changes in connectivity generate periods where local and global genetic diversity reach unexpected values that can be maintained over thousands of generations and can strongly bias the estimation of the effective population size and the interpretation of neutrality tests. Finally we discuss how such processes can explain observed macro-evolutionary patterns of species diversity and its implication in the estimation of nowadays genetic diversity. Our results are thus directly relevant to the evolution of populations and provide guidelines for the management and conservation of natural populations

POWER TESTING OF NEUTRAL THEORY

Omar Al Hammal
Leeds University, United Kingdom

It is currently accepted that different processes controlling species abundances can generate the same community-level patterns. Whether or not such patterns can be used to discriminate between underlying mechanisms structuring communities is still controversial. Here we show a power test that can determine the sample size needed to distinguish between alternative processes, from niche to neutral, represented in different stochastic community models. This can allow designing experiments with the right sampling effort and contribute to improve our knowledge of the mechanisms that shape communities.

STOCHASTIC METACOMMUNITY THEORY: LINKING ECOLOGICAL DRIFT, DISPERSAL LIMITATION AND NICHE-DRIVEN DYNAMICS

David Alonso
Spanish Institution for Scientific Research (CSIC), Spain

The main goal of community ecology is to understand the underlying forces that shape species assemblages. As Mark Vellend says, only four fundamental processes drive community dynamics: selection, speciation, dispersal, and drift. Classical community ecology emphasizes only the first of these processes: community structure is determined by the ability of species to adapt to, create, and be selected for different ecological niches. Neutral theory, instead, considers speciation, dispersal and ecological drift in the absence of species differences. In this talk, I will present a framework to link niche-driven dynamics, dispersal and ecological drift. I will present some examples to analyse the advantages and limitations of this approach.

AMBUSH *VERSUS* CRUISE SEARCH BY A PREDATOR LOOKING FOR ITS PREY

Steve Alpern
London School of Economics, United Kingdom

When searching for a single prey animal in a given region, a predator has two modes: (i) active, or cruise search, and (ii) ambush, or sit-and-wait search. Hunting animals are typically categorized by the mode of search they adopt. Some species may adopt either mode, depending on external (visibility, prey density, weather) or internal (hunger) parameters. It has been observed that some species alternate between modes in a single search. Our model explains this alternation of modes as a mixed strategy in an Ambush Search Game. Roughly speaking, the possibility of ambush lessens the likelihood of the prey changing locations during the search, thereby rendering it more susceptible to an exhaustive search in the cruising mode. This version of the search game is a Stackelberg model in which the prey knows the speed at which the predator is moving (the probability of ambush). We show that the optimal probability of cruising search equals the square root of the unsearched fraction of the region, so the predator starts mostly cruising and ends mostly ambushing.

A VERSION OF THE PREDATOR-PREY SEARCH GAME WHERE THE PREDATOR IS SILENT

Robert Arculus
London School of Economics, UK

There has been recent interest in the question of how a predator should optimally alternate between ambushing and cruising when searching for a prey known to be in a confined area. The prey can attempt to change location, but will be captured during the move if the predator is in ambush mode. The recent studies of Alpern et al. assume a "noisy predator", so that the prey always knows the fraction of the search area that has already been explored. Conversely, our model assumes a "silent predator", so that the prey can only surmise the extent of the current exploration. We also include a parameter that represents a commitment by the predator to inspect the entire space by a certain time, which can be interpreted as representing a degree of impatience. To make the problem tractable, we assume the search space consists of discrete "cells", and that capture takes place either when predator and prey occupy the same cell, or when the prey randomises which cell it occupies while the predator is ambushing. As well as calculating general upper and lower bounds on the expected time until capture, we explicitly solve the game for some simple cases; among other results, we show that with a patient searcher and a search space consisting of two cells, the expected capture time is equal to the square of the golden ratio. We also provide a conjecture for the value of the game in the general case with a patient predator. Further results, as well as support for the conjecture, are obtained through numerical techniques. Note that the game need not be interpreted strictly in a "search" context: for instance, it can also be related to the question of when prey should time an attempt to flee against an unseen but known-to-be-approaching predator.

IN WHICH CURRENCY ARE PAID PAYOFFS IN EVOLUTIONARY GAMES?

Krysztof Argasinski
University of Sussex, United Kingdom

In the standard approach to evolutionary games and replicator dynamics, differences in fitness can be interpreted as an excess from the mean Malthusian growth rate in the population. In the underlying reasoning, related to an analysis of "costs" and "benefits", there is a silent assumption that fitness can be described in some kind of "units". However, in most cases these units of measure are not explicitly specified. Then the question arises: are these theories testable? How can we measure "benefit" or "cost"? A natural language, useful for describing and justifying comparisons of strategic "cost" versus "benefits", is the terminology of demography, because the basic events that shape the outcome of natural selection are births and deaths. Here we present the consequences of an explicit analysis of births and deaths in an evolutionary game theory framework. We will investigate different types of mortality pressures, their combinations and the possibility of trade-offs between mortality and fertility. We will show that within this new approach it is possible to model how strictly ecological factors such as density dependence and additive background fitness, which seem neutral in classical theory, can affect the outcomes of the game. We consider the classical example of the Hawk-Dove game, and show that when reformulated in terms of our new approach surprising new details and biological predictions are produced.

COMPETITION PROCESSES, A TOOL TO MODEL PATHOGEN ADAPTATION TIME

Romain Bourget
LAREMA, France

In many biological contexts, humans try to control harmful populations by introducing resistance into their habitat. However, this strategy is rarely durable because of swift pathogen adaptation to a new hostile environment. Multi-resistance is thought to be a way to delay pathogen adaptation. To understand the population adaptation to multi-resistance, we were interested in the impact of the structure of multi-resistant environment on the waiting time before emergence of a multi-virulent mutant. We formulated a stochastic population model based on competition processes with mutation, migration and recombination. We included a fitness cost for mutants overcoming resistance. To estimate the emergence time, we performed numerical simulations in which we vary pathogens life history traits and the environment structure. The numerical simulation showed the strong dependence of the emergence time on the environment structure. In the case of diversified environment including mono-resistant and susceptible areas, emergence time is a parabolic function of the fraction of resistant area. The emergence time was longer for low and high resistant area fractions, because of induced low migration and mutation probabilities. For multi-resistant environment, emergence time increases with the increase of number of resistances and with the decrease of the transition environments proportion. The results of the model provide insight into our understanding the interplay between used disease control strategy and the pathogen evolution rate to overcome the resistance. The model can be used for designing control strategies preventing rapid adaptation of harmful populations.

SOME MISTAKES GO UNPUNISHED: THE EVOLUTION OF "ALL OR NOTHING" SIGNALLING

Mark Broom
City University London, UK

Many models of honest signalling, based on Zahavi's handicap principle, predict that if receivers are interested in a quality that shows continuous variation across the population of signallers, then the distribution of signal intensities will also be continuous. However, it has previously been noted that this prediction does not agree with empirical observation in many signalling systems, where signals are limited to a small number of levels despite continuous variation in the trait being signalled. Typically, there is a critical value of the trait, with all individuals with trait values on one side of the threshold using the same cheap signal, and all those with trait values on the other side of the threshold using the same expensive signal. It has already been demonstrated that these classical models naturally predict such "all-or-nothing signalling" if it is additionally assumed that receivers suffer from perceptual error in evaluating signal strength. We show that such all-or-nothing signalling is also predicted if receivers are limited to responding to the signals in one of two ways. We suggest that many ecological situations (such as the decision to attack the signaller or not, or mate with the signaller or not) involve such binary choices.

CAN IT BE WORTH DELAYING REPRODUCTION IN A STEADY ENVIRONMENT?

John Bryden
University of London, United Kingdom

Delaying reproduction is, on the face of it, a counterproductive strategy. One would expect those organisms with the fastest growth to invade a population. That said, work has shown how it can be worth delaying reproduction to accumulate resources to help offspring through an early vulnerable phase (Trivers 1974), making a social contribution to offspring (Lion & Van Baalen 2009, Bryden 2010), or through bet hedging when the environment means there are large fluctuations in population size (Tuljapurkar 1990). It's not clear what the best strategy is in a steady environment when a population is at equilibrium. I model this by considering a simple organism that accumulates resources before reaching a reproduction threshold where it divides into two new organisms. Each individual in the model pays a cost of living each time step and encounters discrete resources stochastically in the environment with a probability based on the density of the population. An individual's resource level thus follows a biased random walk either reaching the low threshold (where it dies), or the reproduction threshold. With reproduction, resources are shared equally with offspring after paying a cost of reproduction. This system can be modelled with a backward equation by separating the timescale of an individual's lifetime from that of changes in environmental resource availability. I solve this equation to give the fitness of a small number of invading mutant individuals with a different reproductive threshold to that of a population at equilibrium, showing that there is an optimal reproduction threshold based on minimising the amount spent on the cost of reproduction. I then consider cases where there is a trade-off for the reproductive threshold against living and reproductive costs. The results can be applied to microbial ecology and can serve as a baseline for more detailed models.

ON EMERGENCE TIMES OF COMPETITION PROCESSES

Loïc Chaumont

Université d 'Angers, France

Competition processes are natural extensions of birth-death processes in higher dimensions. At any time, for any type, a birth, a death or a mutation to another type can occur. This work is concerned with the time *S* at which a particular type emerges in the population (through spontaneous birth or mutation). We give some bounds for the tail of the distribution of *S*. Then, using properties of quasi-stationary distributions, we give conditions for the existence of an initial law under which *S* is exponentially distributed. Finally, we provide some examples of applications to the emergence time of pathogen mutants overcoming host resistance in a host-pathogen system.

A GENERAL MODEL OF GENETIC DIVERSIFICATION BY POSITIVE AND NEGATIVE CORRELATED PLEIOTROPIC INTERACTIONS

Dan Cohen

The Hebrew University of Jerusalem, Israel

A directed change in the selection regime on any one allele or fitness component increases the frequency and expression of all the alleles with positively correlated pleiotropic fitness effects, and decreases the frequencies and expression of the complementing alleles with negatively correlated pleiotropic effects, in proportion to their correlations with the selected fitness. The increased frequencies and expressions of the positively correlated subset of alleles are expected to reinforce the fitness of the alleles in the positive subset in subsequent generations by positive feed back interactions, and to increase further the forces of selection at the same selection regime. Opposite reinforcing effects are expected in the negatively correlated subset. Continuing selection at a constant selection regime is expected therefore to amplify the genetic divergence between the distributions of any initial subsets of positive or negative correlations between the pleiotropic effects of the alleles. A selected or random establishment of any particular set of alleles is expected to cause an increase over many generations of the frequency and expression and the strength of the correlations of all the phenotypically equivalent positively correlated pleiotropic alleles in all the genes, which will increase further and establish the selective advantage and the irreversibility of the initially established alleles, and the divergence between randomly initiated intra specific and inter specific genetic changes. Such processes may generate much of the observed irreversible genetic and ecological diversification between species and lineages in changing selection regimes. Several representative examples will be presented.

THE EFFECTS OF RECRUITMENT STRATEGY ON THE BENEFITS OF POLYDOMY IN ANT COLONIES

Zoe Cook, Dan Franks & Elva Robinson
University of York, United Kingdom

A polydomous ant colony is one in which the population exists in at least two spatially separated but socially connected nests. The individuals of the colony function as one unit and there is regular interchange of individuals and of resources between nests. It has been suggested that the main benefit of polydomy may be an increase in foraging efficiency due to the ability to carry out dispersed-central place foraging. Several previous models and empirical studies support this hypothesis. The theoretical arguments for this hypothesis are based on ants foraging independently; however, part of the success of many ant species is their ability to recruit large numbers of workers to food sources. Recruitment may be in the form of tandem running, group recruitment, or long or short term pheromone trails. Decentralisation of the colony through polydomy may affect the success of recruitment by limiting the interactions between ants based in separate nests. We have developed an agent-based model which extends previous models by incorporating both indirect mass recruitment via pheromone trails and direct recruitment through group foraging. The model is used to investigate the interaction between recruitment behaviour and polydomy under varying resource distributions. The results are interpreted in terms of the energy budget of the colony, the time spent locating food, and the time used in recruitment. When a single food is present monodomous colonies perform equally well or significantly better than polydomous colonies when recruitment is used. When food is dispersed polydomy is significantly more successful except when group foraging is used. The results highlight the importance of interactions between recruitment, colony size, and colony organisation and provide several empirically testable predictions.

ANALYTICAL PROPERTIES OF SPECIES AREA CURVES IN SPATIAL NEUTRAL MODELS

Stephen Cornell
University of Leeds, United Kingdom

Spatially explicit neutral theory gives an interesting null model for species area curves (SACs), explaining the triphasic nature of SACs in terms of dispersal, mutation, and drift. However, while many quantities such as spatial moments can readily be calculated for this type of model, the computation of SACs is much more challenging. O'Dwyer and Green (Ecology Letters 13:87-95 (2010)) recently proposed a formula using field theoretical methods adapted from physics, but their results have not been verified independently. I shall present a different analytical approach for studying this problem, using a Kolmogorov backward equation for a model in continuous space without a local zero sum. Using this method, we can derive the analytical behaviour of the SACs at large or small areas, though a complete solution for the whole regime of areas remains elusive. I will compare these results to simulations both on a lattice and in continuous space, and with O'Dwyer and Green's formula.

MUSSELS ON THE MOVE: HOW LÉVY WALKS EVOLVED IN A SELF-ORGANIZING SYSTEM

Monique de Jager
Netherlands Institute of Ecology, the Netherlands

A lingering problem in animal ecology is to explain animal movement patterns in complex natural systems. Ecological theory explains animal movement by its efficiency in finding resources in an externally given environment, ignoring that animals also shape their habitat by their movement and exploitation. Here, we show that feedback between individual movement behavior and environmental complexity can explain the evolution of scale-free movement strategies in self-organized mussel beds. Laboratory experiments demonstrate that mussels apply a scale-free Lévy walk during the process of spatial self-organization. Using spatially explicit models, we reveal that Lévy movement accelerates pattern formation, which feeds back to improve mussel fitness and consequently explains the evolution of Lévy walks. Our results exemplify that feedback between selection at the individual level and emergence of habitat complexity is crucial for understanding animal movement in natural ecosystems.

ENSEMBLES OF EVOLUTIONARY HISTORIES: ADAPTATION, SIMULATIONS AND INFERENCE

Harold de Vladar
IST Austria, Austria

A path ensemble describes all the possible histories that a population can follow between two states at two time points. Each history η has an associated probability proportional to the factor Exp[-$NA_{(\eta)}$], where N is the size of the population and A comprises three terms: Fisher's information, fitness flux, and the additive genetic variance that has been accumulated during the history. In a sense, these three quantities measure the degree of adaptation of a population. Surprisingly, although these quantities have been discovered more or less independently, they combine to weight a population's history in a relatively simple framework. The methods of path ensemble bring together distinct aspects of evolutionary genetics, the most important being measures to the speed of adaptation, the Wright-Fisher model, diffusion of allele frequencies, and the evolution of quantitative traits and their genetic variance, among other aspects. Furthermore, it complements Adaptive Bayesian Computation and Monte Carlo methods by introducing an efficient way to implement simulations conditional on data, and also leads to Maximum Likelihood estimators for selection.

EPIDEMIOLOGY OF OVERTREATMENT IN VECTOR-BORNE DISEASES

Cornelis Drost, C.J. Thomas & J.G.P. Gamarra
IBERS, Aberystwyth University, United Kingdom

Drug resistance in horizontally-transmitted vector-borne diseases is a substantial hindrance to our attempts to control such diseases. Among the potential factors influencing the rates at which resistance develops, the stability of resistant strains within the population, and their ability to spread, overtreatment of the population - unnecessary treatment of uninfected individuals due to misdiagnosis - is an overlooked and potentially critical factor. Misdiagnosis already has many known consequences, including wasted resources, unnecessary exposure to drugs, and failure to treat the actual disease being misdiagnosed. It is however, highly prevalent in many areas of marginal transmission, where diseases with similar early symptoms are often mistaken by under equipped clinics and wrongly treated. Specifically for malaria, a lack of treatment is considered too great a risk even if a diagnosis cannot be made. In these epidemical, low transmission areas, drug resistance often first emerges before spreading to endemic areas. Via a simple SI model, we track the dynamic dependence on overtreatment of resistant and wild-type disease strains within a community. We show that, besides the deleterious effects of overtreatment on the spread of drug resistance, the long term consequences of earlier resistance far outweigh any short term reduction in morbidity. In low transmission areas, the cost of this trade off becomes critical, and triggers resistance spreading to neighbouring endemic areas. We conclude that overtreatment is an unnecessary risk that should not be overlooked in control programs of some vector borne diseases. Given some of the cheap new equipment aiming to reduce misdiagnosis and through proper training of clinicians, reduction of overtreatment is a feasible and affordable crucial goal.

A NICHE-BASED MECHANISM FOR NEUTRAL-LIKE PATTERNS

Xiaoguang Du
University of Groningen, the Netherlands

The debate on the role of species differences in shaping biodiversity patterns, with its two extremes of pure niche theory and neutral theory, is still on-going. It has been demonstrated that a slight difference in competitive ability of species severely affects the predictions of the neutral model. At the same time, neutral patterns seem to be ubiquitous. Here, we model both negative density dependence (NDD) and competitive asymmetry (CA) simultaneously. Our simulation results show that an appropriate intensity of NDD can offset the negative effect of CA (modelled as fecundity difference) on species coexistence and produce a neutral-like species abundance distribution. Therefore, our model provides a plausible mechanistic explanation of neutral-like patterns, but contrary to the neutral model, a species' relative abundance is positively related to its competitive ability in our model.

PHENOLOGY DRIVES MUTUALISTIC NETWORK STRUCTURE AND DIVERSITY

Francisco Encinas Viso
University of Groningen, the Netherlands

Several network properties have been identified as determinant for the stability and complexity of mutualistic networks. However, the mechanisms that give rise to these network properties are still unclear. Phenology seems important, because it shapes the topology of mutualistic networks, but its effects on the dynamics of mutualistic networks have scarcely been studied. Here, we study these effects with a general dynamical model of mutualistic and competitive interactions where the interaction strength depends on the temporal overlap between species that results from their phenologies. We find that phenologies maximizing mutualistic interactions and minimizing intra-guild competitive interactions generate speciose, nested and poorly connected networks with moderate asymmetry, but low resilience. Moreover, lengthening the season increases asymmetry, thereby augmenting diversity and resilience. This highlights the fragility of real mutualistic communities with short seasons (*e.g.,* Arctic environments) to drastic environmental changes because of their low resilience.

MAKING INFERENCES ON DIVERSIFICATION FROM MOLECULAR PHYLOGENIES

Rampal Etienne
University of Groningen, the Netherlands

Because of the incompleteness of the fossil record, molecular phylogenies are often the only source of information we have on historical diversification. Therefore, we need methods that can extract this information efficiently. Here I outline a general method that calculates the likelihood of the phylogenetic branching times given a model of diversification and illustrate it with some examples of data and models.

EQUATION OVERLOAD: WHAT DETERS EMPIRICAL BIOLOGISTS FROM CITING THEORETICAL WORK?

Tim Fawcett
University of Bristol, United Kingdom

Most research in biology is empirical, yet empirical studies rely fundamentally on theoretical work for generating testable predictions, particularly in ecology and evolution. A cursory reading of the literature, however, reveals that many empirical studies build largely on other empirical studies, with little direct reference to relevant theory. This observation suggests a failure of communication between theoreticians and empiricists. To investigate this problem systematically, we gathered citation data for papers published in the top three journals specialising in ecological and evolutionary research: *Proceedings B*, *American Naturalist* and *Evolution*. We analysed how the number of times a paper is cited is affected by its use of equations, which reflects the technical level of the model description. We found that the number of equations per page has a significant negative impact on citation rates, with equation-heavy papers being cited less frequently. However, against this general trend, the number of citations by other theoretical papers actually increases with the number of equations per page, though only slightly. Overall, more effective communication to other theoreticians, via a technical model description involving the increased use of equations, is outweighed by less effective communication to empiricists. This creates a conflict, since mathematical models obviously cannot dispense with equations and other technical aspects. Is there any way that theoreticians can communicate their work better to a broad biological audience, consisting largely of empiricists? We repeated the above analyses, this time distinguishing between equations in the main text and those in appendices. A high density of equations in the main text significantly reduces citation rates, whereas the density of equations in the appendices has no effect. This suggests a simple strategy for communicating theory more effectively to empiricists: where possible, place your technical model descriptions in an appendix.

THE EFFECTS OF ECOLOGY ON A WEB-STEALING SPIDER

Meghan Fitzgerald
University of Wisconsin Madison, USA

The Argyrodes subfamily of spiders contains a number of species that are kleptoparasitic (steal prepared food items and/or web space from host spiders). Based on the method they employ for stealing, the subfamily has been spilt into species groups. One of these, the Argyrodes species group, generally chooses hosts that are large, with large webs, and is an obligate parasite on its host both by stealing food and eating the silk of the web. They live with their host, supposedly having very minimal impact on the host because of the asymmetry in their sizes, for as long as their host is available. We have made a simulation exploring the interaction between the chosen host and a kleptoparasite, which behaviourally follows the pattern found in the Argyrodes species group. Specifically we have used a model to determine the effects of a number of parameters on this interaction, such as the number of kleptoparasites to occupy a single web, the amount of food available, the amount of damage the kleptoparasites do to the web, and the implication of environmental impact on the web, assuming that at some point the host should abandon the web and start over in another location. The finding of this simulation will be used to determine the overall ecology of this behavioural interaction and allow field testing from a new perspective.

MULTIPLE NICHES FOR AGONISTIC BEHAVIOURS CAN EMERGE FROM DYADIC RELATIONSHIP

Matthias Franz
Courant Research Centre "Evolution of Social Behaviour" Göttingen, Germany

Agonistic behaviours are important fitness determinants because they regulate access to limited resources. The possibility that repeated interaction among individuals can lead to dyadic relationships, i.e. dyad-specific behavioural patterns, has been largely ignored in attempts to understand the evolution of agonistic behaviours. This strongly limits our understanding of the evolutionary basis of agonistic behaviours and resulting consequences for animal and human societies. We addressed this problem with an evolutionary, agent-based model that was based on the "sequential assessment game". This model was extended by giving individuals the ability to remember outcomes of past interactions and as a consequence to adjust dyad-specific agonistic behaviours. We investigated evolutionary dynamics for different values of contestable resources and recorded resulting behavioural patterns at the dyad and group level. We found that two distinct behavioural strategies evolved: (1) a reinforcing strategy that led to the establishment of stable subordinate-dominance relationships and despotic societies and (2) an alternating strategy that led to the establishment of relationships in which the roles of being dominant and subordinate switch constantly and from which egalitarian societies emerged. While for large benefit values only the reinforcing strategy evolved, for small values both strategies were evolutionarily stable. Evolutionary stability emerged because both strategies created different social environments with differentiated selection pressures. This finding contradicts the fundamental assumption in animal socio-ecology that only unique niches for social behaviours exist and, thus, demonstrates that the ability to form dyadic relationships can lead to more complex evolutionary dynamics than previously anticipated. In addition, we propose extensions to existing socio-ecological frameworks regarding the impact of phylogeny and cooperative mechanisms of resource partitioning.

QUANTIFYING INTROGRESSION RISKS IN RANDOM ENVIRONMENTS WITH HAZARD RATES

Atiyo Ghosh
Leiden University, the Netherlands

Introgression is the permanent incorporation of genes from the genome of one population into another. Since the advent of genetically modified crops, quantifying the risk of introgression has become of increasing concern, since it has already been established that crops readily hybridise with their wild relatives. Introgression itself is riddled with many stochastic elements, from randomness in the number of offspring of different plants, and the number of hybrids produced per harvest, to the changing weather through the seasons. Furthermore, it can be shown that introgression will occur almost surely in the long run, but the question remains as to how long, and to find a suitable measure of risk. In this talk, the hazard rate is proposed as a measure of risk in such scenarios. The hazard rate of an event is the probability per unit time that it occurs in that time, given that it has not previously occurred. The multiple layers of stochasticity are captured in a branching process model.

SOME CAUSES OF THE VARIABLE SHAPE OF FLOCKS OF BIRDS

Charlotte Hemelrijk
University of Groningen, the Netherlands

The variations in shape in the aerial displays of huge flocks of starlings (*Sturnus vulgaris*) above the sleeping site at dawn is amazing. Also other species of birds are highly variable in the shape of their flocks, more so than fish schools; fish schools are usually oblong. The causes of this variability, however, are hardly known. We investigate these causes with the help of a model of the self-organization of a traveling group. In the present paper, we use a model, called StarDisplay, whose flocking patterns resemble qualitatively and quantitatively those of real birds, in particular starlings. In it, individuals coordinate with nearby others through attraction, alignment and avoidance (just as in models of fish schools). This is supplemented with some specifics of starling behaviour, namely 1) their aerial locomotion, 2) a low and constant number of interaction-partners and 3) preferential movement above a `sleeping area'. As to shape, we measure the relative proportions of the flock and the longest dimension in respect of its direction of movement. We show that flock shape is usually more variable when local differences in movement in the flock are larger. This happens when a) flock size is larger, b) interacting partners are fewer, c) the flock turnings are stronger, and d) individuals roll into the turn. In contrast to our expectations, when variability of speed in the flock is higher, its shape and the positions of its members are more static. We explain this and indicate the adaptive value of low variability of speed and spatial restriction of interaction and develop testable hypotheses.

EFFECTS OF COSTS OF ENERGY RESERVES ON BODY SIZE AND ADIPOSITY

Andrew Higginson
University of Bristol, United Kingdom

The storage of lipids to buffer energy shortage may have ecological costs such as increasing locomotive costs or vulnerability to predation, and animals may be more muscular in order to reduce such costs. If muscle mass and lipid mass interact to determine survival, then both the proportional protein content (muscularity) and proportional lipid storage (adiposity) of animals will be affected by factors such as skeletal size and food availability. Here, we explore how optimal adiposity and muscularity may depend on such factors. We confirm the expectation that adiposity should decrease with the risk of predation and increase with the risk of interruptions to the food supply. More surprisingly, we find that the predicted relationships between skeletal size, muscularity, and adiposity qualitatively depend on various factors: for example, adiposity should increase with foraging energy costs. We predict that if the locomotive costs of carrying lipids are low then adiposity should increase with total body mass, whereas if such costs are high then adiposity should decrease with total body mass. These predictions are supported by cross-species comparisons of adiposity. Our approach demonstrates that broad patterns of body composition can be understood in terms of the fundamental ecological trade-off between starvation and predation and provides testable predictions for between- and within-species comparisons.

THE CO-EVOLUTION BETWEEN MUTUALISM AND CONDITION-DEPENDENT EMIGRATION AND IMMIGRATION

Aniek Ivens
University of Groningen, the Netherlands

Mutualism, cooperation between individuals of different species, is wide-spread throughout nature and vital to ecosystem stability. From an evolutionary perspective, however, these interactions are poorly understood. Where two partner species live closely together, typically, the partner's interests will never be fully aligned. The stable mutualisms we observe in nature might therefore be the result of on-going conflict rather than harmonious cooperation. What mechanisms promote mutualism evolution and govern their evolutionary stability? A potential battleground for conflict between mutualistic partners is dispersal. The role of dispersal is ambiguous: it requires the dispersing partner to allocate energy towards dispersal rather than towards productivity, but dispersal also has strong stabilizing potential. Indeed, in the form of condition-dependent dispersal it allows dispersing individuals to actively choose cooperating partners (immigration) and avoid non-cooperative individuals (emigration). We present an integrative mechanistic model for the co-evolution between investment into mutualism and condition-dependent dispersal (including both immigration and emigration) in a patch-structured population. The model enables us to assess the importance of dispersal for the evolution of mutualisms. Our evolutionary models on mutualism are inspired by a particular kind of mutualisms, cultivation mutualism. In these interactions, a host species promotes the growth of its symbiont species. Examples include ants culturing fungus in their nest for food or ants farming aphids for honeydew. Especially the latter case of aphid-tending ants has been a source of inspiration, as it is the biological system which also has been focus of our empirical work on mutualism. This combined theoretical and empirical approach will hopefully further contribute to a more general understanding of the evolution of mutualism.

SOCIAL LEARNING AND EVOLUTION IN A STRUCTURED ENVIRONMENT

Daniel Jones
Goldsmiths University of London, United Kingdom

We survey the relationships between evolution, individual learning and social transmission within mixed and structured environments. With a novel individual-based simulation, we determine the regimes under which each mode of learning dominates, in terms of the environment's relative complexity and its rate of change. We show that social learning can give rise to a particularly potent form of the “Baldwin effect'', wherein an organism develops an innate trait having first acquired it socially. We demonstrate that social learning is of increased significance in a structured environment.

EMPIRICAL EVIDENCE FOR LÉVY SIGNATURES IN MUD SNAIL MOVEMENT

Andrea Kölzsch
Netherlands Institute of Ecology (NIOO-KNAW), the Netherlands

While moving through the landscape animals should optimize their foraging efficiency. How they accomplish this task is yet generally unclear and may depend on different internal and external factors. If food is rare and animals have limited information of their surroundings, foragers have been hypothesized to move randomly with fat tailed step length distributions, often referred to as Lévy walks. In contrast to previous studies we didn't test this hypothesis with tracks of wild animals, but examined foraging movement of a simple organism in the lab. We studied the foraging patterns of mud snails (*Hydrobia ulvae*) in different experimental landscapes in which 10% was covered with algae. Algae distributions in space were chosen to be either random, regular or fractal. As control we examined snail movement on bare mud and fully covered algae landscapes, respectively. We determined and analysed the snails' step length and turning angle distributions using high frequency recordings of their positions. Step length distributions of individual snail movement on bare, fully covered and fractal landscapes show fat tails, often being well fit by truncated power laws. On random and regular landscapes snail tracks resemble Lévy walks less well, but approximate Brownian walks. Additionally, movement is clustered on food patches as well as on bare mud, but snails seem to reorient after food encounter and move slower when feeding on a patch of algae. Our results clearly show the prominence of Lévy motion under spatially homogeneous conditions, pointing out that Lévy walks are a baseline movement strategy for mud snails. The comparison with movement in different, heterogeneous landscapes indicates that these Lévy walks are modulated to Brownian walk-like patterns by frequent food encounter. Moreover, our results suggest that the Lévy walk strategy is most efficient in fractal landscapes, which resembles food distributions encountered in their natural habitat.

MODELLING THE ECOLOGY OF SYMBIONT-MEDIATED PROTECTION AGAINST PARASITES

Marek Kwiatkowski
ETH Zürich/Eawag, Switzerland

There is increasing evidence that some maternally transmitted symbionts protect their hosts against parasites, thus ensuring their own persistence. Despite the protection they provide, such symbionts are typically found only in a fraction of the host population. This suggests that symbiont-conferred resistance is costly, and/or that the maternal inheritance of symbionts is not perfect. To investigate these hypotheses and other properties of this complex ecological system, we develop a computational model based on the example of bacterial endosymbionts that protect aphids against parasitoid wasps. Simulations show that, in the absence of more complex effects, a very fine balance between costs of harbouring symbionts and the strength of protection they provide is required to maintain coexistence of protected and unprotected hosts. These constraints are significantly relaxed and coexistence becomes a common outcome if deployment of symbiont-provided defences upon a parasite attack entails an additional (induced) cost. Transmission rates of symbionts also affect coexistence, which is more frequently observed under high (but not perfect) fidelity of vertical and low rates of horizontal transfer. Finally, we show that the prevalence of defensive symbionts has a strong influence on the population dynamics of hosts and parasites: population sizes are stable if and only If the protected hosts dominate.

CUMULATIVE CULTURE: TRANSMISSION FIDELITY IS THE KEY TO THE BUILD-UP OF COMPLEX CULTURE IN HUMANS

Hannah Lewis
University of St. Andrews, United Kingdom

While many animals have evolved socially transmitted behavioural traditions, human culture appears unique with respect to cumulative culture, whereby cultural knowledge and technology accrues diversity and complexity over time. Previous theoretical analyses suggest that high-fidelity transmission has the potential to create a greater number of cultural traits that exist for longer within a population, supporting the hypothesis (Tomasello 1994) that transmission fidelity is central to cumulative culture. In principle, accurate transmission leading to trait persistence potentially provides time during which complex or beneficial modifications may occur, known as the process of ‘ratcheting’. However, this verbal argument has never been formally evaluated. Here we use simulation models to test whether increasing trait fidelity, and hence longevity, within a cultural group leads to cultural ratcheting, and thereby facilitates cumulative culture. We also explore the roles and relative importance of novel invention (generation of entirely new traits), modification (e.g. refinement of existing traits), and combination (the bringing together of two established traits to generate a new trait) in the build-up of cumulative culture. Our results show that small increases in transmission fidelity, leading to greater trait longevity, can result in a massive build-up of complex cultural traits. In comparison, modification and combination have a lesser influence on, and novel invention appears unimportant to, the ratcheting process. Our findings support the idea that high-fidelity transmission is the key driver of human cumulative culture.

OPTIMAL TIMING OF REPRODUCTION IN A WARMING WORLD

Marjolein Lof
Netherlands Institute of Ecology (NIOO-KNAW), the Netherlands

Spring temperatures have increased since the 1980's. Plants, insects and vertebrates all responded differently in their phenology to this temperature increase, resulting in phenological mismatches between species. For many species there is only a short period in the annual cycle during which the conditions are favourable for reproduction and thus such a mismatch can have major fitness consequences. We study the effect of climate change on the timing of reproduction, using the great tit, *Parus major*, as our model organism. Great tits have not advanced their laying date while the peak date of the caterpillar biomass (the main food source for their young) has advanced with two weeks. To understand how current and future climatic variables affect the degree of phenological mismatch we developed a dynamic state model that incorporates year-to-year variation in daily temperatures and caterpillar biomass to find the optimal laying date for different temperatures. In the model the birds' decision depends on the time of year, the current temperature, the food availability, the brood size and the age of the brood. We parameterized this model for the great tits and the caterpillar biomass of our long-term study population at the Hoge Veluwe (The Netherlands). We found that, due to higher spring temperatures, the optimal laying date for different temperatures has changed.

THE GENERALITY OF INCLUSIVE FITNESS THEORY

James Marshall
University of Sheffield, United Kingdom

Inclusive fitness theory, summarised in Hamilton’s rule, is a dominant explanation for the evolution or social behaviour. A parallel thread of evolutionary theory holds that selection between groups is also a candidate explanation for social evolution. The mathematical equivalence of these two approaches has long been known. Several recent papers, however, have objected that inclusive fitness theory is unable to deal with strong selection or with non-additive fitness effects, and concluded that the group selection framework is more general, or even that the two are not equivalent after all. Yet, these same problems have already been identified and resolved in the literature. In this talk I will survey these contemporary objections and examine them in the light of current understanding of inclusive fitness theory.

COOPERATION AND THE EVOLUTION OF INTELLIGENCE

Luke McNally
Trinity College of Dublin, Ireland

Understanding the evolution of social learning strategies and biases is the key to developing a complete account of both the evolution of our capacity for cumulative culture and the way that the content of that culture itself changes over time. One way to study this is to test alternative strategies in evolutionary simulations to understand what kind of learning we expect natural selection to favour. The first social learning strategies tournament (Rendell et al. 2010 Science) helped us to understand why social learning itself is adaptive, but was based on a relatively simple model. In this poster we give details of the second social learning strategies tournament, to be run in 2011/2012, which extends this model in three ways. Firstly we allow for the evolution of model-based learning biases by giving agents the option to select from available learning models based on information about them. Secondly we introduce a cumulative dimension to the evolution of the simulated cultures by allowing agents to select a move that results in a refinement, which increases the payoff of an existing behaviour. Finally, we introduce a more realistic population structure by setting the simulation in a meta-population of three demes linked by small numbers of migrants. A total of 25,000 Euro is available as prize money for the best performing strategies. More details can be found at http://lalandlab.st-andrews.ac.uk.

ECO-EVOLUTIONARY DYNAMICS OF ADAPTIVE AND NON-ADAPTIVE RADIATIONS IN SUPER NETWORKS

Carlos Melian
Centre for Ecology, Evolution and Biogeochemistry (EAWG), Switzerland

Large data sets, experimental and theoretical studies on the origin of radiations have shown the role of genetic, sexual, ecological and geographical processes. Most empirical data suggest ecological speciation driven by adaptations to niches is the dominant force triggering radiations, yet there is a lack of theory (1) inferring in the same framework the mechanisms driving radiations and the macro-ecological patterns of biodiversity, (2) predicting the large variation in occurrence and extent of radiations between taxa and between localities of the same taxon, and (3) identifying whether this variation comes from genetic, reproduction mode or ecological mechanisms or some combination of these processes. In the present talk I aim to (1) introduce DNA-sequence-based eco-evolutionary models of interacting networks (i.e. mating and spatial graphs or mating graphs and trophic food webs) to generate patterns of diversity, (2) compare the models with genetic, sexual, ecological and geographical mechanisms using two of the largest individual-based food webs to date: (1) The Guadalquivir estuary food web, southern Spain, with 100,000+ individuals sampled in different environmental conditions, and (2) The biodiversity inventory from the "Area de Conservacion Guanacaste" in northwest Costa Rica with 450,000+ caterpillars, their parasites and host plants collected since 1978. These two data sets have also independent estimations of abundance and present sufficient levels of resolution and number of species to permit inference at individual, species and community levels simultaneously. We show that, in addition to adaptive processes, like negative frequency-dependent selection driven by niche adaptation, non-adaptive processes like sexual selection, mutation and genetic-ecological drift may be playing an important role in generating and maintaining biodiversity patterns in interacting networks.

MATHEMATICAL NICHE THEORY

Géza Meszéna
Eötvös University, Hungary

We provide a mathematical formulation of niche theory. Our basic theorem states that robustness of species coexistence against parameter perturbations depends on the species' segregation with respect to their population regulation: They have to be sufficiently different in their densities' differential impact on and their growth rates' differential sensitivity towards the “regulating variables”, the environmental variables involved in the feedback loop of population regulation. Therefore, one has to identify the “niche space” with the index set of the regulating variables. The partitioning of the niche space (i.e., the niches of the individual species) is given by the impacts and sensitivities, as the operationalization of the resource utilization function.

We demonstrate that a weak departure from neutrality generically cannot be compensated by weak niche segregation; therefore the alleged continuum between neutral and niche-based coexistence does not exist. The possibilities for niche segregation can be classified as functional, habitat and temporal - or a combination thereof; the last two have nontrivial technical issues. Spelling out our niche concept for structured populations provides the connection between the niche description of the whole population and of the i-states. If the populations are spatially structured, one ends up with the description of niche segregation between different habitats. The key point is that the same kind of regulating factor behaves as a different regulating variable when located at different habitats. Analogously, in the case of environmental fluctuations one has to deal with variable population size and consider the regulating variables at different instants of time as different. Chesson's coexistence-maintaining effects of “relative nonlinearity” and “storage effect” can be interpreted in this context. A structured metapopulation model can deal with the situation of successional niche segregation.

EVOLUTIONARY DYNAMICS OF DN/DS

Carina Mugal
Uppsala University, Sweden

The ratio of divergence at non-synonymous and synonymous sites, dN/dS, is a widely used measure in comparative genomics analyses to study the efficacy of selection acting on codon evolution. Originally applied to distantly related sequences, the dN/dS ratio is supposed to represent the ratio of fixed non-synonymous to synonymous differences between independent lineages, where dN/dS is a function of the effective population size and the selection coefficient. However, when applied to sequences from recently diverged populations the impact of shared ancestral polymorphisms as well as segregating polymorphisms on the dN/dS measure might be substantial. At short timescales, the proportion of polymorphic sites compared to fixed differences is high and artificially inflates estimates of divergence. The duration of the inflation depends on the effective population size and the strength of selection. As the strength of selection on non-synonymous and synonymous polymorphisms differs, estimates of dN/dS might be considerably biased by polymorphisms at short timescales. Moreover, it has recently been shown, that in a pure population genetics context the dN/dS ratio is rather insensitive to the selection coefficient. Hence, the use of the dN/dS measure for inferences on the efficacy of selection acting on codon evolution is precarious for recently diverged lineages. To address this issue, we investigate the performance of dN/dS in a population genetics framework and its development over time after population divergence. We simulate the evolution of codon sequences along a speciation event at variable divergence times to examine the evolutionary dynamics of dN/dS and its dependence on divergence time. Additional analytical investigations of the expected value of the dN/dS ratio and its variance assist in understanding the influence of polymorphisms on dN/dS. Finally, comparison of simulated and analytical results to standard comparative genomics approaches helps in interpreting estimates of dN/dS in comparative genomics studies of recently diverged species.

OF SPECIATIONS AND EXTINCTIONS - EVOLUTIONARY DIVERSIFICATION UNDER SEASONALLY VARYING REPRODUCTION

Mario Pineda-Krch
Centre for Mathematical Biology, Canada

Reproductive phenology, the timing of recurring reproductive events, is of fundamental importance in determining individual fitness and ultimately the evolutionary fate of a population. While countless studies document how reproductive phenology varies across altitudinal and latitudinal environmental gradients and the fitness costs associated with variations and mismatches in reproductive phenology, no studies have addressed the effect of variation in reproductive phenology on evolutionary diversification. Previous theoretical and empirical studies have focused either on the evolution of the phenological trait, e.g. the evolution of reproductive timing and synchrony, or on evolutionary responses in traits with environmentally driven selection pressures, e.g. adaptation to changing climatic conditions. Here we show that net evolutionary diversification is significantly reduced when recruitment occurs during short yearly pulses, e.g. as found at high latitudes. This reduction is due to a trade-off between an increased speciation rate and increased extinction probability for daughter species that occurs during short recruitment periods. We use a simple model integrating a novel combination of a pre-existing eco-evolutionary model for resource competition with variation in recruitment. Our theory identifies within-season variability in reproductive phenology as a novel and pervasive ecological mechanism that fundamentally influences sympatric evolutionary diversification by modulating speciation rates and extinction probabilities. These results conform to recent findings showing a faster turnover of species at high latitudes and provide a first example of a plausible ecological mechanism for the latitudinal diversity gradient.

MAINTENANCE OF BIRD SONG DIALECT BORDERS

Bob Planqué
VU University Amsterdam, the Netherlands

Many bird species, especially song birds but also for instance some hummingbirds and parrots, have noted dialects. By this we mean that locally a particular song is sung by the majority of the birds, but that neighbouring patches may feature different song types. Behavioural ecologists have been interested in how such dialects come about and how they are maintained for over 45 years. As a result, a great deal is known about different mechanisms at play, such as dispersal, assortative mating and learning of songs, and there are several competing hypotheses to explain the dialect patterns known in nature. There is, however, surprisingly little theoretical work testing these different hypotheses at present. We will start with the simplest kind of model in which one may speak of dialects, and which takes into account the most important biological mechanisms: one where there are but two patches, and two song types. It teaches us that a combination of little dispersal and strong assortative mating ensures dialects are maintained. The role of learning is more elusive, but we will show in what way frequency dependent learning may contribute to song dialect maintenance.

EMERGENCE OF COALITIONS, THEIR RECIPROCATION AND THEIR EXCHANGE IN A MODEL

Ivan Puga-Gonzalez
University of Groningen, the Netherlands

In most primate societies individuals help others in fights by forming coalitions. Since supporting another is risky, it has been argued, for instance in the theory of reciprocal altruism, that a supporter should receive a benefit in return (e.g. support or grooming). Evidence for reciprocation of support and for its exchange for grooming has indeed been found in several primate studies. However, the cognitive processes underlying reciprocation and exchange are debated: they may involve record keeping or simpler cognitive processes. What simple processes may suffice is still an open question. In this study, we show that patterns of coalition may emerge by self-organization in an individual-based model. In the model, GrooFiWorld, individuals group and when meeting each other they decide whether to fight, groom or rest, but they do not intentionally form coalitions. Yet, in our model coalitions are observed when in two consecutive events, two different individuals fight against the same victim by mere coincidence. Moreover, in the model, reciprocation of support and the exchange of grooming for being supported and support for being groomed emerge as a side-effect of social facilitation, attack being risk-sensitive and patterns of spatial proximity among individuals. Our model shows that little cognition is needed to generate these coalition patterns. The model can be used as a null-model for the generation of hypotheses to be studied in real primates.

A MODEL OF SINGLE-SIDED MATE CHOICE BASED ON MULTIPLE TRAITS

David Ramsey
University of Limerick, Ireland

It has been observed that a female fiddler crab follows a two-step procedure when deciding to mate. First, she observes the size of the male and then if he is sufficiently large, she will investigate his burrow. Suppose a female is presented with a (potentially infinite) sequence of prospective mates. The *i*-th male is presented at moment *i*. She can observe two traits, whose values are denoted X_1 and X_2. The value of a male is given by $V = X_1 + X_2$. The search costs of the female are split as follows: *c* is the cost of finding a male (incurred at each moment), the cost of observing cue *i* is c_i, $i = 1, 2$. On finding a male, the female first observes cue 1. At this point she can take one of three possible decisions: i) accept the male, ii) observe cue 2, iii) reject the male and continue searching. After observing cue 2, the female must decide whether to accept or reject the male. The net reward of a female from searching is assumed to be the value of the male chosen minus the total sum of costs incurred. It is assumed that X_1 and X_2 come from a joint normal distribution, the marginal distribution of X_i is N(μ_i, σ_i^2), $i = 1, 2$ and the coefficient of correlation between X_1 and X_2 is ρ. This talk will present a method for deriving the optimal strategy of a female searcher. Cue 2 should never be observed when $c_2 \geq \sigma_2\sqrt{1-\rho^2}/\sqrt{2\pi}$. The potential gains from such sequential observation of traits compared to always observing one cue (or always observing both cues) is investigated. Also, the question of which cue should be observed first is addressed. It should be noted that, e.g. in the context of fiddler crabs, it may be natural to assume that cue 2 must be observed before a male is accepted, i.e. on observing cue 1 a female cannot choose option i) above. The form of the optimal strategy in this problem is derived and compared to the form of the optimal strategy in the original model.

MODELLING THE HYDRODYNAMICS OF INFINITE SCHOOLS OF FISH

Daan Reid
University of Groningen, the Netherlands

Experimental evidence indicates that fish may increase their hydrodynamic efficiency by swimming in groups. However it is unclear how this increase is achieved. Theoretical predictions concerning infinitely large schools state that for optimal efficiency, fish should position themselves in a rigid diamond-shaped structure in horizontal layers, with specific inter-individual distances. However, these theoretical predictions ignore several factors such as viscosity and the shape of the fish. Empirical studies of the hydrodynamics of fish are difficult, labour-intensive and do not allow accurate measurements of the forces of swimming (i.e. thrust and drag). For these reasons computer models of hydrodynamics can be of great help, in which forces and flow can be measured directly, and the position and movement of the fish can be controlled. In this talk, we apply such a method, called Multiparticle Collision Dynamics, in order to study undulatory swimming of fish in infinite schools. We investigate four different configurations, namely a diamond-shaped lattice, a rectangular lattice, an infinitely long line and an infinitely wide phalanx. We vary the distance among individuals and we compare efficiency, swimming speed, thrust and power “wasted'' sideways among the different structures and a single fish. We find that fish swim more efficiently in schools than alone. Unexpectedly, swimming in an intact wake of a predecessor increases both speed and efficiency. Having lateral neighbours increases efficiency and reduces swimming speed. Remarkably, the benefits are lowest for the specific diamond configuration that was predicted to be optimal.

BIODIVERSITY AND DIETARY DIVERSITY IN MARINE FOOD WEBS

Axel Rossberg
Queen's University of Belfast, UK

This study aims at explaining the observation that the size-distribution of the relative proportions that prey species contribute to the diets of fish (and some squid) is the same for marine communities across the oceans. In particular, dietary diversity is independent of local biodiversity (Rossberg et al., 2011, Proc R Soc B, 278:1617). It is shown that this observation can be reproduced in a Lotka-Volterra assembly model. An analytic solution of this model reveals the underlying mechanism, operative in scenarios of fierce predation: if diets were broader, a fish population's resources would exclude each other through indirect competition. Thus, the trophic niche widths of fish constrain sustainable biodiversity among their prey. The coupling of marine species richness to the latitudinal gradient of solar irradiance appears to result from the evolution of trophic niche widths to a point where competitive overlaps are minimized while retaining some dietary diversity. The joint feasibility of these mechanisms in complex food webs is demonstrated by simulation experiments.

THE ROLE OF HERBIVORES AS ECOSYSTEM ENGINEERS ON LAWN-BUNCH MOSAIC FORMATION

Jasper Ruifrok
University of Groningen, the Netherlands

Many grazed landscapes consist of lawn-bunch mosaics, i.e. patches of short grasses of high palatability (lawn) and patches of tall vegetation of low palatability (bunch). Due to their high heterogeneity, these landscapes hold high biodiversity and consequently have a high conservational value. While much research has focused on the maintenance of grazing lawns due to self-facilitation by herbivores (grazing keeps vegetation short, which increases palatability, which stimulates grazing), little is known about the formation of these mosaics. The aim of this study is to understand the role of herbivores as ecosystem engineers (i.e. modifiers of their physical environment by changing the levels of abiotic stress by compacting the soil), on the formation of these landscapes, using a modelling approach. We first identified how grazing intensity and abiotic stress affected lawn formation. We found that lawn formation is positively influenced by grazing intensity. Surprisingly, lawn formation was also positively influenced by abiotic stress. At high levels of abiotic stress it is easier for herbivores to keep vegetation short and thus palatable. We used this information to make a simple spatial model in which grazing intensity is a function of the palatability. We found that in a landscape with patches of abiotic stress lawn-bunch mosaics could emerge. Next we implemented hierarchical decisions of herbivores and soil modification by herbivores in our spatial model. Soil compaction by herbivores increases the levels of abiotic stress. Due to hierarchical decision making of herbivores abiotic stress became spatial dependent, forming patches of stress, in which lawns were formed. Consequently, herbivores can create a heterogeneous lawn-bunch mosaic from homogenous conditions by ecosystem engineering. We believe that due to the generality of the assumptions of our model, our findings apply to a large range of grazed ecosystems, from topical savannahs to temperate wood pastures to tundra.

POPULATION DYNAMIC CONSEQUENCES OF INTERACTIONS AMONG LIFE STAGES OF INSECTS

Sinha Somdatta
Centre for Cellular& Molecular Biology, India

Density-dependent feedbacks play a major role in shaping the population densities of organisms over several generations. In insect species, the multiple life cycle stages (*e.g.*, egg, larva, pupa, and adult), having different morphological, physiological and behavioural traits within a single generation, experience different types of developmental and environmental feedback processes to regulate their life history characteristics (*e.g*., body size, fecundity, etc) and numbers. The regulation is highly nonlinear and interacts across different stages, thereby influencing the evolution of population densities of the adult insect over several generations. A long standing problem with many insect species is that they exhibit a hump-shaped egg-to-adult transition, which essentially means that the same number of adults can arise from two widely different egg numbers - a one to two mapping problem, which confound development of population dynamic models of these insect species. In this work, this problem is addressed with the life cycle of the fruit fly, *Drosophila melanogaster*. There are three major density-dependent regulations that govern *Drosophila* population sizes - (i) *Larval competition on larval survival*, (ii) *Larval competition* and (iii) *Adult crowding effect - on female fecundity*. A highly nonlinear dependence of larval density on adult body size and its consequent influence on female fecundity also seems to play a significant role. Considering these density-dependent mechanisms a discrete population dynamic model is formulated. Simulation of the model shows a variety of dynamics in population size - from stable to chaos - for different parameter values. The model is tested on four different laboratory data sets of *Drosophila* populations raised in different combinations of larval and adult food regimes. This study contributes significantly to the understanding, and consequently to prediction, of adult population size variation in organisms such as, insects, by delineating the interactions among the different life stage characteristics.

ASYMMETRIC HELPING AND HARMING BEHAVIOUR

Peter Sozou
London School of Economics, UK /RWTH Aachen University, Germany

Kin selection has selected for helping behaviours between relatives. Conversely, when there is competition for a resource and an individual's chance of winning the competition increases if its opponents are weaker, selection may favour harming behaviour. This study considers a competition between two relatives for a reproductive reward. Each individual is characterised by a condition variable, termed its strength. A stronger individual has a greater chance of winning the competition, and also higher expected reproductive output conditional on winning the condition. This may lead to a situation whereby on the one hand helping behaviour increases an individual's expected benefit through kin selection if the opponent wins, while on the other hand harming behaviour increases its own chance of winning the competition. This study will characterise the conditions for asymmetric helping and harming behaviour, whereby individual A helps individual B while at the same time individual B harms individual A.

FIXED AND DILUTABLE BENEFITS: FEMALE CHOICE FOR GOOD GENES OR FERTILITY

Sam Tazzyman
University College London, United Kingdom

Benefits accruing to females who exercise mate choice have been defined to be either “direct” or “indirect”. We suggest an alternative distinction: benefits can be considered “fixed”, meaning they are on average equal to all females mating with the same male (for example good genes benefits) or “dilutable”, meaning they are shared between females mating with the same male, so that the more mates a male has the lower the average benefit to each (for example fertility benefits or many forms of direct benefit). Using a simple model we show that this distinction has a major effect on the form of female preference. We predict that mating skew will be far greater in species where the benefits are fixed compared to those where the benefits are dilutable.

IN-SILICO EVOLUTION OF DEVELOPMENTAL NETWORKS FOR BODY PLAN SEGMENTATION AND DIFFERENTIATION

Kirsten ten Tusscher
University of Utrecht, the Netherlands

A key question in evolutionary-developmental biology (evo-devo) is how the complex organisms we see around us have evolved and how the developmental programs producing this complexity are encoded in the genome. Data show that neither genome size nor gene numbers correlate strongly with organismal complexity. Instead, a similar set of genes, the so-called developmental toolkit, is used for development in organisms of widely different complexity. However, in more complex organisms these genes do seem to have more intricate spatiotemporal expression patterns, suggesting increased regulatory complexity. Thus, a major focus in evo-devo is on the role of regulatory network architecture. Here we use a simulation model to study the evolution of gene regulatory networks involved in body plan patterning. We study the combined evolution of body plan segmentation and differentiation. This allows us to study whether modular networks evolve. Modularity of developmental networks is suggested to be essential for robustness and evolvability, and hence for enabling evolution of ever more complex body plans. Furthermore, body plan segmentation and differentiation are key developmental innovations. Our simulations show that both modular and non-modular developmental networks can evolve, but that indeed the modular networks are more robust and evolvable. However, in contrast to previous ideas, this network modularity is hard to detect in network architecture, while clearly present in network dynamics and functioning. Furthermore, earlier studies always investigated the evolution of segmentation or differentiation in isolation. We find, as a free side effect of studying their combined evolution, that the in-silico evolved developmental networks are strikingly similar to naturally observed axial patterning mechanisms. Finally, we use our model to shed light on the evolutionary transition from the ancestral, sequential mode of body axis patterning used in basal insects to the highly derived, simultaneous patterning mode used by *Drosophila*.

THE ECOLOGICAL RATIONALITY OF STATE-DEPENDENT VALUATION

Pete Trimmer
University of Bristol, United Kingdom

Laboratory studies on a range of animals have identified a bias which seems to violate basic principles of rational behaviour: a preference is shown for feeding options which previously provided food when reserves were low, even though another option had been found to give the same reward with less delay. The bias presents a challenge to normative models of decision-making (which only take account of expected rewards and the state of the animal at the decision time). To understand the behaviour, we take a broad ecological perspective and consider how valuation mechanisms evolve when the best action depends upon the environment being faced. We show that in a changing and uncertain environment, state-dependent valuation can be favoured by natural selection: individuals should allow their hunger to affect learning for future decisions. The valuation mechanism that typically evolves produces the kind of behaviour seen in standard laboratory tests. By providing an insight into why learning should be affected by the state of an individual, the paper provides a basis for understanding psychological principles in terms of an animal's ecology.

DIATOM-SEDIMENTATION FEEDBACK GENERATES A SELF-ORGANISED GEOMORPHIC LANDSCAPE ON INTERTIDAL MUDFLATS

Johan van de Koppel
Netherlands Institute of Ecology, the Netherlands

During spring, intertidal flats can exhibit strikingly regular spatial patterns of diatom-covered hummocks alternating with almost bare, water-filled hollows.

We hypothesize that 1) the formation of this geomorphic landscape is caused by a strong interaction between benthic diatoms and sediment dynamics, inducing spatial self-organization, and 2) that self-organization affects ecosystem functioning by increasing the net average sedimentation on the tidal flat. We present a combined empirical and mathematical study to test the first hypothesis. We determined how the sediment erosion threshold varied with diatom cover and elevation. Our results were incorporated into a mathematical model to investigate whether the proposed mechanism could explain the formation of the observed patterns. Our mathematical model confirmed that the interaction between sedimentation, diatom growth and water redistribution could induce the formation of regular patterns on the intertidal mudflat. The model predicts that areas exhibiting spatially-self-organized patterns have increased sediment accretion and diatom biomass compared with areas lacking spatial patterns. We tested this prediction by following the sediment elevation during the season on both patterned and unpatterned parts of the mudflat. The results of our study confirmed our model prediction, as more sediment was found to accumulate in patterned parts of the mudflat, revealing how self-organization affected the functioning of mudflat ecosystems. Our study on intertidal mudflats provides a simple but clear-cut example of how the interaction between biological and geomorphological processes, through the process of self-organization, induces a self-organized geomorphic landscape.

THE EVOLUTIONARY ECOLOGY OF PLANT PATHOGENS

Femke van den Berg
Rothamsted Research, UK

The evolutionary responses of plant pathogens to the use of fungicides and/or resistant crops have been intensively studied. The selection pressures imposed on the evolution of a pathogen's life-cycle characteristics by other disease management strategies or changes in the environment have been studied much less frequently. Such adaptations can, however, have a major effect on epidemic dynamics and therewith host performance. This presentation aims to give an overview of theoretical and experimental approaches, with their associated challenges, that have recently been undertaken in a BBSRC-INRA collaboration. One of the major challenges in evolutionary ecology of plant pathogens is designing suitable experiments to detect trade-off relationships between pathogen life-cycle dynamics. Using three examples I will show that despite these challenges progress is under way. It will then be shown how these trade-offs can be incorporated into mathematical models to answer specific evolutionary questions. A trade-off between infection efficiency and inter-season survival was used to study whether such a seasonal trade-off can explain branching into two genetically distinct yet coexisting pathogen phenotypes. A similar trade-off was subsequently used to show that an increased period of host absence between two consecutive growing seasons can select for either an increased or a decreased reproductive capacity. In a next example it is shown that a trade-off between a pathogen's latent period and its associated spore production might result in the selection of a shortened latent period when the ratio of auto-infection to allo-infection is high. Finally, data analysis revealed a cultivar specific relationship between lesion size and spore production. In this talk it will be shown that such cultivar specific relationships can lead to the erosion of quantitative resistance through traits that are not related to the breaking of resistance.

THE PREDICTIVE ADAPTIVE RESPONSE: A LIFE HISTORY MODEL OF *BICYCLUS ANYNANA*

Joost van den Heuvel
University of Leiden, the Netherlands

The predictive adaptive response (PAR) is a hypothesis that explains the development of age related disease in humans from an evolutionary perspective. It is suggested that early nutritional status (in the womb) acts as a cue to direct development towards an optimal phenotype, which influences health later in life. The applicability of this concept to human life histories has been hampered by lack of convincing datasets that show the effect. In contrast, insects which live in seasonal environments are more suitable for testing the validity of the basic concepts of PAR. For instance, we have manipulated the larval and the adult stage environment of the tropical butterfly *Bicyclus anynana* in the laboratory. Individuals that were restricted in food during the larval stage coped better with forced flight during the adult stage compared to individuals with an optimal larval stage, suggesting that this phenotypic plasticity enhanced fitness. We have tested whether this response could be adaptive in a field situation using an energy allocation model. All stages of the life history of the butterfly were modelled, and the optimal state dependent strategic decisions were calculated using dynamic programming. This allowed us to test whether in specific seasons the behaviour of the individuals as observed laboratory could be adaptive in natural environments. The results from the model confirmed that the wet season individuals coped better with flight stress when they were restricted in nutrition during early development compared to individuals with an optimal larval stage, which was facilitated by altered allocation patterns during the pupal stage. We conclude that for *B. anynana* early stage cues can direct development towards an optimal phenotype that influences life history later in life. In the future state dependent modelling could be used to study whether developmental plasticity is adaptive for longer-lived species with less predictable environments.

EVOLUTION OF COOPERATIVE FORAGING: SELF-ORGANIZATION AND PATCH DEPLETION

Daniel van der Post
University of Groningen, the Netherlands

Many animals live in groups. One proposed reason is that grouping allows cooperative food finding. Based on optimal foraging models however, the present consensus is that grouping cannot increase food intake rates. These models assume discrete food patches which are fully detectable. Here, we use a spatial individual-based model where food patches are aggregates of food items beyond the scale of individual perception. We allow foraging and grouping behaviour of individuals to evolve in environments with different resource distributions, where neither patch detection, grouping, nor cooperative foraging are directly assumed. We show that grouping can evolve to increase food intake rates. Two kinds of grouping evolve: traveling pairs and opportunistic grouping where individuals only aggregate when feeding. Grouping evolves because it allows individuals to better detect and deplete patches. This is particularly true for fragmented patches, which are especially difficult for solitary foragers to deplete. Solitary foragers often leave a patch prematurely because they cannot see the whole patch. In groups, individuals that are still eating allow other individuals that inadvertently leave the patch, to return and continue feeding. In this way grouping leads to a shift in niche specialization allowing individuals to better exploit partially depleted patches. Under certain conditions niche differentiation allows solitary and grouping individuals to co-exist on the single resource. This group foraging can be seen as cooperative in the sense that together individuals can achieve more than on their own. However, there is no cooperative dilemma as individuals cannot avoid producing information for their neighbours. Moreover, cooperation is not encoded in genes as an individual-level strategy. Instead, cooperation exists as a group-level process generated by the interaction between grouping and the environment. By not predefining cooperative foraging, we find that it evolves outside of a cooperative dilemma setting via multi-level selection.

THE EVOLUTION OF GENERALIZED RECIPROCITY ON SOCIAL INTERACTION NETWORKS

Sander van Doorn & Michael Taborsky
University of Bern, Switzerland

Generalized reciprocity ("help anyone, if helped by someone") is a minimal strategy capable of supporting cooperation between unrelated individuals. Its simplicity makes it an attractive model to explain the evolution of reciprocal altruism in animals that lack the information or cognitive skills needed for other types of reciprocity. Yet, generalized reciprocity is anonymous and thus defenseless against exploitation by defectors. Recognizing that animals hardly ever interact randomly, we investigate whether social network structure can mitigate this vulnerability. Our results show that heterogeneous interaction patterns strongly support the evolution of generalized reciprocity. The future probability of being rewarded for an altruistic act is inversely proportional to the average connectivity of the social network when cooperators are rare. Accordingly, sparse networks are conducive to the invasion of reciprocal altruism. Moreover, the evolutionary stability of cooperation is enhanced by a modular network structure. Communities of reciprocal altruists are protected against exploitation, because modularity increases the mean access time, *i.e.*, the average number of steps that it takes for a random walk on the network to reach a defector. Sparseness and community structure are characteristic properties of vertebrate social interaction patterns, as illustrated by network data from natural populations ranging from fish to primates.

THE EVOLUTION AND COEXISTENCE OF HERBIVORES UNDER BETWEEN-PLANT COMPETITION

Ellen van Velzen
University of Groningen, the Netherlands

Consumer-resource models have been used extensively to study the evolution and coexistence of generalist and specialist herbivores. However, current models do not take into account competition between plants, or include only intraspecific competition phenomenologically with, for example, a logistic growth function. Here we mechanistically incorporate competition in an existing two-resource model, by setting the total amount of nutrients (free or contained in consumers and resources) to a fixed value. We find a much more diverse spectrum of evolutionary outcomes than did previous models: in addition to the three combinations of generalists and specialists found in previous models, we find five other evolutionary outcomes, depending on the strength of the consumer trade-off. Furthermore, which outcomes are most likely to occur strongly depends on the plant intrinsic growth rate and on the total amount of nutrients in the system. Thus, our results suggest that the realistic assumption of a fixed amount of nutrients may explain the multitude of strategies in real systems.

THE EVOLUTION OF INDIVIDUAL VARIATION IN COMMUNICATION STRATEGIES

Franjo Weissing & Carlos Botero
University of Groningen, the Netherlands

Communication is a process in which senders provide information via signals and receivers respond accordingly. This process relies on two coevolving conventions: a “sender code” that determines what kind of signal is to be sent given the sender’s state; and a “receiver code” that determines the appropriate responses to different signal types. By means of a simple but generic model, we show that polymorphic sender and receiver strategies emerge naturally during the evolution of communication, and that the number of alternative strategies observed at equilibrium depends on the potential for error in signal production. Our model suggests that alternative communication strategies will evolve whenever senders possess imperfect information about their own quality or state. These findings provide an explanation for recent reports of individual differences in communication strategies, and suggest that the amount of individual variation that can be expected in communication systems depends on the type of information being conveyed. Our model also suggests a link between communication and the evolution of animal personalities, which is that individual differences in the production and interpretation of signals can result in consistent differences in behaviour.

TO OWN OR TO OWN NOT: A GAME THEORY MODEL OF RESOURCE OWNERSHIP AND DEFENCE

Lev Yampolsky
East Tennessee State University, USA

Organisms face decisions about taking an ownership of a resource and defending it vs. sharing a common pool of resources with the rest of the population. Examples like the evolution of territoriality and female guarding emphasize the role of the trade-off between effective guarding private resources and exploiting shared resources. In the presence of such trade-off and in the absence of direct benefits of ownership it is difficult to explain invasions of Owner/Defender strategies into ancestral populations of non-owners. Previous theoretical work demonstrated that the ownership strategy can be an ESS if the owner of a patch of resources is the first to arrive on it, a result known as the prior residency effect. We investigate different scenarios of competition for a patchy resource with random distribution of individuals into patches and predict the outcome of competition of different types of Owner/Defender strategies with the non-owner (Offender, O) strategy. In the case of Conditional Defender strategy (cD: own and defend the patch of resources only if you have prior residency, otherwise play the Offender strategy) both the cD and O can be the ESS and an unstable equilibrium between the two pure strategies can exist. In the case of the Unconditional Defender strategy (uD: own and defend a patch of resources no matter what) there is a range of parameters under which neither the uD nor O strategies are the ESS, and a stable equilibrium exists. These outcomes are confirmed in an individual-based model representing these scenarios. Incorporation of D’s ability to increase defence efficiency in response to Offenders’ frequency results in an extended range of parameters predicting an evolutionary stable mixed strategy.

FIREOX: AN SIR MODEL TO DESCRIBE THE SPREAD OF SMOULDERING PEATLAND FIRE

Jon Yearsley
University College of Dublin, Ireland

Peatlands are globally important ecosystems. They are estimated to contain a third of the world's terrestrial carbon, but smouldering fire is an increasing threat to the ecosystem services provided by peat lands. Although the theory of smouldering combustion is surprisingly poorly developed, recent experimental data are characterising the behaviour of smouldering peat fire across a range of environmental conditions (e.g. moisture and O_2 availability). We present the development of a simple, cellular automaton SIR model that assimilates these data and characterises the large scale behaviour of a smouldering fire. The model predicts the final proportion of burned fuel given an expected rate of spread and rate of fuel consumption. The model has been initially applied to the prevalence of smouldering wildfires during the past 350 million years of Earth history. Results show a threshold concentration of oxygen (18-19%) below which fire prevalence is extremely low, which points to a period of Earth history when fire activity was likely to have been exceedingly uncommon.

POSTERS

SPECIES DIVERGENCE BASED ON STATISTICAL AND EVOLUTIONARY MODELS

Mansour Aliabadian, Niloofar Alaie kakhki & Jamshid Darvish
Ferdowsi University of Mashhad, Iran

The barn owl, *Tyto alba* (Scopoli 1769), occurs worldwide and shows a considerable amount of morphological and geographical variation, leading to the recognition of many subspecies around the world. But comprehensive studies about this species are yet to be done. Statistical and evolutionary models for morphological characters and mitochondrial genes *(CYTB)* are analysed for 31 individuals around the world. We used Maximum likelihood (ML), maximum parsimony (MP) and Bayesian analysis to show genetic variation between the *alba* clade (old world) and *furcata* clade (new world) and to compare their topology. All statistical and evolutionary models suggest that barn owls of the Old World may be a separate species from those of the New World.

A VERSION OF THE PREDATOR-PREY SEARCH GAME WHERE THE PREDATOR IS SILENT

Robert Arculus
London School of Economics, UK

There has been recent interest in the question of how a predator should optimally alternate between ambushing and cruising when searching for a prey known to be in a confined area. The prey can attempt to change location, but will be captured during the move if the predator is in ambush mode. The recent studies of Alpern et al. assume a "noisy predator", so that the prey always knows the fraction of the search area that has already been explored. Conversely, our model assumes a "silent predator", so that the prey can only surmise the extent of the current exploration. We also include a parameter that represents a commitment by the predator to inspect the entire space by a certain time, which can be interpreted as representing a degree of impatience. To make the problem tractable, we assume the search space consists of discrete "cells", and that capture takes place either when predator and prey occupy the same cell, or when the prey randomises which cell it occupies while the predator is ambushing. As well as calculating general upper and lower bounds on the expected time until capture, we explicitly solve the game for some simple cases; among other results, we show that with a patient searcher and a search space consisting of two cells, the expected capture time is equal to the square of the golden ratio. We also provide a conjecture for the value of the game in the general case with a patient predator. Further results, as well as support for the conjecture, are obtained through numerical techniques. Note that the game need not be interpreted strictly in a "search" context: for instance, it can also be related to the question of when prey should time an attempt to flee against an unseen but known-to-be-approaching predator.

THE DIRECT AND INDIRECT EFFECTS OF FIRES ON FOREST ECOSYSTEMS

Roland Byron & Karsai Istvan
East Tennessee State University, USA

One of the most important factors in forest ecosystem dynamics is commonly fires. These fires have direct detrimental effects on organisms by burning them and have long term effects on the organisms because the fires restructure the forest and alter the habitats (by destroying the trees) of the animals. We modeled an abstract simple ecosystem consisting of a single species of tree and forest animal that's breeding and survivorship is dependent upon the trees. A model was developed in Netlogo (an agent based modeling and simulations system). Our goal was to have a minimum complexity model. Trees were reproducing by seeds which landed randomly on the habitat. Trees provided fuel for the fire and only died by fire. The animals in the forest moved randomly and had a natural lifetime. They were able to breed when the tree density around a given individual was high. Animals were also subject to death by fire. The effects of the fires were modeled by the random occurrence of annual fires. Dispersion of the fires is dependent upon the place of initiation and the amount of fuel available (trees), which corresponded to the density of the trees (the higher the density the greater chance of dispersion). Using the technique called "parameter sweep" we tested several hypotheses of how fires affected the forest ecosystem directly and indirectly. The main parameters we changed were the number of potential fire initiations per year and the reproductive abilities of the trees. This study shows that the fires have considerable effects on the forest ecosystem. These fires resulted in strong population size decreases in both trees and forest animals and sometimes drove one or both of the populations to extinction. Forest with a higher tree reproduction commonly resulted in the extinction of the animals.

MULTIPLE NICHES FOR AGONISTIC BEHAVIOURS CAN EMERGE FROM DYADIC RELATIONSHIP

Matthias Franz
Courant Research Centre “Evolution of Social Behaviour” Göttingen, Germany

Agonistic behaviours are important fitness determinants because they regulate access to limited resources. The possibility that repeated interaction among individuals can lead to dyadic relationships, i.e. dyad-specific behavioural patterns, has been largely ignored in attempts to understand the evolution of agonistic behaviours. This strongly limits our understanding of the evolutionary basis of agonistic behaviours and resulting consequences for animal and human societies. We addressed this problem with an evolutionary, agent-based model that was based on the “sequential assessment game”. This model was extended by giving individuals the ability to remember outcomes of past interactions and as a consequence to adjust dyad-specific agonistic behaviours. We investigated evolutionary dynamics for different values of contestable resources and recorded resulting behavioural patterns at the dyad and group level. We found that two distinct behavioural strategies evolved: (1) a reinforcing strategy that led to the establishment of stable subordinate-dominance relationships and despotic societies and (2) an alternating strategy that led to the establishment of relationships in which the roles of being dominant and subordinate switch constantly and from which egalitarian societies emerged. While for large benefit values only the reinforcing strategy evolved, for small values both strategies were evolutionarily stable. Evolutionary stability emerged because both strategies created different social environments with differentiated selection pressures. This finding contradicts the fundamental assumption in animal socio-ecology that only unique niches for social behaviours exist and, thus, demonstrates that the ability to form dyadic relationships can lead to more complex evolutionary dynamics than previously anticipated. In addition, we propose extensions to existing socio-ecological frameworks regarding the impact of phylogeny and cooperative mechanisms of resource partitioning.

SCALING EFFECTS IN OPTIMISATION OF SEARCH BEHAVIOUR

Geerten Hengeveld
Netherlands Institute of Ecology (NIOO-KNAW), the Netherlands

Foraging behaviour is hypothesised to be optimised to maximise intake rate. Foraging is a process that takes place at many scales: patches of food need to be found, choices between potential food types need to be made and levels of depletion of local food need to be decided upon. Although optimal behaviour for each of these scales is calculated, little research has focused on the effect of behaviour on one scale on the optimal behaviour on another scale. Especially when constraints limit behaviour on one scale to be optimal, the optimal behaviour on another scale can change. We show that the optimal behaviour when searching for patches of food is altered when suboptimal patch depletion decisions are made. Especially we show that Lévy walks with a Lévy-exponent of 2 are optimal when patch depletion is suboptimal, whereas more ballistic searches are optimal when patch depletion is near-optimal.

EVOLUTION OF SELF-ORGANIZED DIVISION OF LABOUR IN SOCIAL INSECTS

Oleksandr Ivanov
University of Groningen, the Netherlands

Division of labour is one of the most basic and widely studied aspects of colony behaviour in social insects. However, the mechanisms that lead to the emergence of self-organized division of labour remain puzzling. Several models have been proposed in attempt to reveal potential mechanisms of division of labour, but they lack realism and evolutionary perspective. We introduce an evolutionary perspective by modelling the evolution of worker behaviour underlying self-organized division of labour. Each worker is endowed with a neural network that processes incoming information and determines the behaviour (foraging, brood care, staying idle). The properties of the neural network are transmitted by the reproductive of a colony to their offspring. Networks producing the most adequate response to the colony needs have a selective advantage and will be evolutionarily successful. Our results indicate that three factors are necessary for the evolution of division of labour: renewal of colony's workers due to their birth, senescence and death, age perception by workers, and environmental pressure. It was not possible to evolve division of labour without birth and death of workers. When workers renewal was introduced, division of labour evolved, provided that workers could perceive their age. If foraging carried high risk of death, division of labour evolved in a form of age polyethism where young workers performed brood care and older ones foraged. This pattern corresponds to observations in many social insect species. Under low death risk for foragers, a pattern of age polyethism evolved where young workers typically foraged, and cared for brood later in life, like solitary insects do. This study is an example when environmental unpredictability forces biological system to evolve complex phenomenon, division of labour in form of age polyethism. Necessity of division under increased risk of death during foraging might force individuals to group and evolve sociality.

PARADOX OF THE CICHLIDS

Thijs Janzen
University of Groningen, the Netherlands

The young age and high diversity of the cichlids in the three African rift lakes has amazed biologists, ecologists and evolutionary researchers for many years. Lake Tanganyika is deeper, older, and has a more complex bathymetry than the other two lakes. Ecological and evolutionary theory tells us that it should have the *most species* of the three lakes, but it has the *fewest*. To explain the lack of diversity in Lake Tanganyika we will make use of spatially explicit individual based simulations. We will develop a general model assessing the influence of environment size, environment shape and environment stability on biodiversity. Using this general model we will be able to make predictions on the African rift lake system, incorporate specifics of the African rift lakes and make accurate predictions about current biodiversity estimates.

GRAZING-INDUCED PRODUCTION OF DMS CAN STABILIZE FOOD-WEB DYNAMICS AND PROMOTE THE FORMATION OF PHYTOPLANKTON BLOOMS IN A MULTI-TROPHIC PLANKTON MODEL

Nicola Lewis
University of Essex, United Kingdom

Volatile info-chemicals including climatically-relevant dimethyl sulphide (DMS) have been suggested to play important roles in the structuring and functioning of marine food webs. Experimenting with complex natural plankton communities or several trophic levels in laboratory microcosms is challenging and, as a result, empirical data confirming the role of DMS in trophic interactions is lacking. Here I consider a model of the interactions between three trophic levels of plankton: phytoplankton, grazing micro-zooplankton and predatory meso-zooplankton. I show that the inclusion of a grazing-induced DMS production term has a stabilizing effect on the system dynamics under the assumption that DMS acts as an info-chemical and increases the rate of meso-zooplankton predation on grazing micro-zooplankton. I further demonstrate how this feedback between trophic levels can potentially lead to the formation of a phytoplankton bloom. The model provides a suitable framework for further study into the possible role of DMS in the ecology of marine food webs beyond its recognised role as a climate-cooling gas.

THE EFFECTS OF CONFORMISM ON THE EVOLUTION OF BEHAVIOUR IN FINITE POPULATIONS

Lucas Molleman
University of Groningen, NL

When individuals can acquire behavioural traits through social learning, transmission biases can determine evolutionary dynamics in a population. The tendency to imitate behaviour of the majority (conformism) can stabilise equilibria in many classes of evolutionary games. We present an event based model to quantify the effects of conformity on the evolution of pure strategies of individuals interacting in a finite population. A diffusion approximation gives a first intuition about the conditions for a rare mutant to increase in frequency. The distribution of fixation probabilities of rare mutants shows that conformity can create a stable equilibrium of strategies that are individually suboptimal but benefit interaction partners. However, such ‘cooperative’ strategies have more difficulty gaining foothold in a population under conformity, where the disadvantage arises both from the evolutionary game as from low initial frequencies. The numerical results are checked with agent based simulations.

WHAT ARE THE ODDS? THE PROBABILITY OF COEXISTENCE

Stuart Natrass
University College London, United Kingdom

Darwinian demons, that maximize all aspects of fitness, do not exist. Instead, trade-offs in performance of different ecological functions occur within a species, and are commonly offered as an explanation for coexistence in natural communities. Single trade-offs between competitive ability and other life history traits have been shown to support a large number of species, as a result of strong competitive asymmetry, where a larger individual has a much greater effect on its smaller neighbour than vice versa. Considering a single competition-fecundity trade-off in a homogeneous environment, where larger individuals have a competitive advantage but produce fewer (larger) seeds per adult, we examine the effect of the form of asymmetry on the likelihood of species coexisting. We show that if small size differences result in large differences in competitive ability, with the smaller individual having nearly no effect on the larger, this single trade-off can support an arbitrarily large number of species. Further, the likelihood of a given number of species coexisting increases with the degree of competitive asymmetry. However, even in the most favourable conditions, high numbers of species coexisting along this trade-off is unlikely

TOWARDS THE MECHANISTIC RELATIONSHIP OF THE RATE/EFFICIENCY TRADE-OFF IN METABOLISM

Bastian Niebel & Guillermo Zampar
University of Groningen, the Netherlands

Several cells, such as *S. cerevisiae, E. coli* or mammalian cells, show different metabolic modes dependent on the nutrient uptake rate. With a low glucose uptake rate they tend to respire, while they ferment when the glucose uptake rate is high. The metabolic modes of fermentation and respiration use different catabolic pathways with different ATP generating “efficiencies”. It was often argued that a trade-off exists between “rate” and “efficiency”. Although this trade-off resembles an intuitive concept, the term “efficiency” is only vaguely defined and the true mechanic relationship of this trade-off remains unclear. Here, as a first step towards unravelling the relationship, we first identify a true thermodynamic quantity for “efficiency”. When defining efficiency as the ratio between the `entropy production rate per substrate uptake rate' and `the maximum entropy production rate that could be achieved by the same substrate uptake rate’ - with the entropy production rate serving as a measure of the non-equilibrium processes within the cell - we found that this efficiency indeed negatively correlates with the substrate uptake rate in *S. cerevisiae* in a trade-off manner. Based on this observation, we tested whether thermodynamics are indeed the mechanistic cause for the rate/efficiency trade-off. We used a constraint-based modelling approach, which incorporates the stoichiometry of the metabolism, the second law of thermodynamics and the entropy production rate, to test our hypothesis. As we found the metabolic mode to change from the highly efficient respiration to the less efficient fermentation with increasing glucose uptake rate, we conclude that thermodynamics is indeed the cause for the rate/efficiency trade-off in metabolism.

EVOLUTIONARY DYNAMICS OF MISGUIDED RECIPROCITY ON CYCLES

Jorge Peña
University of Lausanne, Switzerland

Misguided reciprocity (also known as upstream reciprocity or generalized reciprocity) is one type of indirect reciprocity according to which individuals help someone if they have been helped by somebody else in the past. Here, I study the evolutionary dynamics of misguided reciprocity on cycles by solving a particular instance of the discrete heat equation, a partial difference equation usually used to model diffusion processes. I find critical cost-to-benefit ratios c/b determining whether or not misguided reciprocity is selected against unconditional defection and unconditional cooperation. Such critical cost-to-benefit ratios depend on the specific stochastic process describing the evolutionary dynamics. When the population size tends to infinity, reciprocators are favoured over defectors when $c/b < 1/2$ for the birth-death process, when $c/b < 5/6$ for the death-birth process or when $c/b < 7/10$ for the imitation updating process. This last result is in perfect agreement with previous results obtained using slightly different model assumptions and a different solving technique (Nowak and Roch 2007).

MODELS OF PLANKTON DYNAMICS

Sofia Piltz
University of Oxford, United Kingdom

The purpose of this study is to develop better mathematical models to account for seasonal conditions to help understand the distribution and composition of plankton communities. Phytoplankton is a primary producer in the aquatic food chain. They require sunlight, carbon dioxide (CO_2) and nutrients for growth. A food web consisting of phytoplankton and zooplankton feeding on them is affected by seasonal variations in these resources. Phytoplankton also functions as a biological pump that transfers atmospheric CO_2 to the ocean. Small and tractable plankton systems are an ideal model system for studying general properties of systems with interacting components which experience external forcing. Traditionally, ecological models have considered the time scale of evolutionary change in traits, such as defence strategies against predators, to be negligible compared to the time scale of the predator-prey interactions. However, it has been shown that ecological and evolutional dynamics are coupled with each other. This kind of rapid adaptation of traits to changing environmental conditions affects ecological interactions and is especially seen in organisms with short lifespan such as species in plankton communities. This work concentrates on the Rosenzweig-MacArthur 1 predator - 1 prey differential equation model (Am. Nat. 97 (1963)) with external forcing included in a periodically varying growth term of the prey. I aim to compare the predicted period of oscillation with the numerical simulation of the forced model. I seek to describe the period of oscillation with an Ordinary Differential Equation (ODE) model by using perturbation theory and method of multiple scales. I will carry out simulations with a model allowing for other parameters to change in time in a seasonal context as a first step towards modeling a larger food network with an adaptive trait approach in seasonally varying environment.

THE EVOLUTION OF COOPERATION BY CULTURAL GROUP SELECTION

Andrés Quiñones
University of Groningen, the Netherlands

The evolution of cooperation in large scale human societies of unrelated individuals is presumably facilitated by culture. Cultural transmission rules like conformism and leadership represent mechanisms that may reduce variation within groups. This facilitates the action of natural selection at the levels of groups, which in turn may favour cooperation. Two different mechanisms have been said to represent selection at the level of groups. Groups with larger proportions of co-operators may produce more migrants, or be less likely to go extinct. Using individual-based simulations I model conformism and leadership under the two scenarios of group selection. By assessing the effect of group size and migration rate, I show that reduced variation within groups alone does not facilitate the evolution of cooperation. The way natural selection acts at the level of groups strongly affects the outcome of evolution. Conformism facilitates cooperation only under a selective mechanism that acts through group extinction. Leadership facilitates cooperation only under a selective mechanism that acts through differential migration. The explanation for cooperation as a cultural trait requires a better understanding of the mechanisms by which individuals acquire traits and how the composition of groups changes over evolutionary time.

THE SECOND SOCIAL LEARNING STRATEGIES TOURNAMENT

Luke Rendell
University of St. Andrews, United Kingdom

Understanding the evolution of social learning strategies and biases is the key to developing a complete account of both the evolution of our capacity for cumulative culture and the way that the content of that culture itself changes over time. One way to study this is to test alternative strategies in evolutionary simulations to understand what kind of learning we expect natural selection to favour. The first social learning strategies tournament (Rendell et al. 2010 Science) helped us to understand why social learning itself is adaptive, but was based on a relatively simple model. In this poster we give details of the second social learning strategies tournament, to be run in 2011/2012, which extends this model in three ways. Firstly we allow for the evolution of model-based learning biases by giving agents the option to select from available learning models based on information about them. Secondly we introduce a cumulative dimension to the evolution of the simulated cultures by allowing agents to select a move that results in a refinement, which increases the payoff of an existing behaviour. Finally, we introduce a more realistic population structure by setting the simulation in a meta-population of three demes linked by small numbers of migrants. A total of 25,000 Euro is available as prize money for the best performing strategies. More details can be found at http://lalandlab.st-andrews.ac.uk.

GEOGRAPHIC PROFILING AS A NOVEL SPATIAL TOOL FOR TARGETING THE CONTROL OF INVASIVE SPECIES

Mark Stevenson
Queen Mary University of London, United Kingdom

Geographic profiling (GP) was originally developed as a statistical tool in criminology, where it uses the spatial locations of linked crimes (for example murder, rape or arson) to identify areas that are most likely to include the offender's residences. The technique has been successful in this field, and is now widely used by police forces and investigative agencies around the world. Here, we show that this novel technique can also be used to identify source populations of invasive species, using their current locations as input. We analyse historical data from the Biological Records Centre (BRC) for 53 invasive species in Great Britain, ranging from marine invertebrates to woody trees, and from a wide variety of habitats (including littoral habitats, woodland and man-made habitats). For 52 out of these 53 data sets, GP outperformed spatial mean, spatial median and centre of minimum distance as a search strategy. We also compared fitted parameter values between different species, groups and habitat types, with a view to identifying general values that might be used for novel invasions where data are lacking. We suggest that geographic profiling could potentially form a useful component of integrated control strategies relating to a wide variety of invasive species and discuss on-going developments in GP theory.

IN-SILICO EVOLUTION OF DEVELOPMENTAL NETWORKS FOR BODY PLAN SEGMENTATION AND DIFFERENTIATION

Kirsten ten Tusscher
University of Utrecht, the Netherlands

A key question in evolutionary-developmental biology (evo-devo) is how the complex organisms we see around us have evolved and how the developmental programs producing this complexity are encoded in the genome. Data show that neither genome size nor gene numbers correlate strongly with organismal complexity. Instead, a similar set of genes, the so-called developmental toolkit, is used for development in organisms of widely different complexity. However, in more complex organisms these genes do seem to have more intricate spatiotemporal expression patterns, suggesting increased regulatory complexity. Thus, a major focus in evo-devo is on the role of regulatory network architecture. Here we use a simulation model to study the evolution of gene regulatory networks involved in body plan patterning. We study the combined evolution of body plan segmentation and differentiation. This allows us to study whether modular networks evolve. Modularity of developmental networks is suggested to be essential for robustness and evolvability, and hence for enabling evolution of ever more complex body plans. Furthermore, body plan segmentation and differentiation are key developmental innovations. Our simulations show that both modular and non-modular developmental networks can evolve, but that indeed the modular networks are more robust and evolvable. However, in contrast to previous ideas, this network modularity is hard to detect in network architecture, while clearly present in network dynamics and functioning. Furthermore, earlier studies always investigated the evolution of segmentation or differentiation in isolation. We find, as a free side effect of studying their combined evolution, that the in-silico evolved developmental networks are strikingly similar to naturally observed axial patterning mechanisms. Finally, we use our model to shed light on the evolutionary transition from the ancestral, sequential mode of body axis patterning used in basal insects to the highly derived, simultaneous patterning mode used by *Drosophila*.

THE EVO-DEVO OF BUTTERFLY WING PATTERNS: A MODELLING PERSPECTIVE

Jordi van Gestel, Patrícia Beldade & Franz J. Weissing
University of Groningen, the Netherlands

Evolutionary developmental biology (evo-devo) seeks to understand how developmental pathways are shaped by evolution and how in turn the course of evolution is affected by these pathways. The eyespot pattern on butterfly wings is an ideal model system to study the interplay between development and evolution, since much is known about their development and the selective forces acting on them. Here we study how the gene regulatory network and developmental patterns underlying eyespot formation evolve. Three important results were observed. First, different gene regulatory networks and, therefore, developmental patterns can generate the same phenotype. Second, even when independent runs were started from the same initial conditions the evolutionary outcome could be completely different due to the accumulation of different neutral mutation. Third, many of the evolutionary transitions are associated with genotypes that are developmentally unstable.

MIGRATION LOAD IN THE MULTI-LOCUS SYSTEMS

Alexey Yanchukov
University of California Santa Barbara, USA

Genetic load due to the immigration of locally disfavoured genotypes can be calculated for the moderate number of loci using first step analysis for the branching process. Assuming immigration of the equally spaced recombining loci on a linear map, the load at equilibrium is just one minus the number of selective deaths caused by the immigrant loci, times the migration rate. We show that such a method allows calculating the load assuming both negative and positive epistasis, and is much faster than simulating the population iteratively to reach the steady state. In certain parts of the parameter space, the load is low for both the small and the large numbers of loci, since the latter are quickly eliminated in blocks in the early stage of introgression. Correspondingly, the load is high for the intermediate number of loci, which have more chances to recombine away from each other and thus cause more selective deaths. I discuss how migration load can be used as a proxy to estimate the power of two different evolutionary processes caused by the gene flow: (i) reinforcement of prezygotic reproductive barriers, or (ii) increase of robustness to the immigrant genetic elements (e.g. dominance of the local alleles over the immigrant).

LIST OF PARTICIPANTS

(K = keynote lecture, T = contributed talk, P = poster)

Name		Institute	Email
Iqra Ahmad		East Tennessee State University, USA	ahmadi@goldmail.etsu.edu
Nicolas Alcala	T	University of Lausanne, Switzerland	Nicolas.Alcala@unil.ch
Omar Al Hammal	T	University of Leeds, UK	O.AlHammal@leeds.ac.uk
Niloofar Alaie kakhki	P	Ferdowsi University of Mashad, Iran	ni_al144@um.ac.ir
Mansour Aliabadian		University of Amsterdam, NL	m.aliabadian@uva.nl
David Alonso	T	CSIC, Spain	d.alonso@ceab.csic.es
Steve Alpern	T	London School of Economics, UK	s.alpern@lse.ac.uk
Robert Arculus	T,P	London School of Economics, UK	rarculus@gmail.com
Krysztof Argasinski	T	University of Sussex, UK	argas1@wp.pl
Homayoun Bagheri	K	University of Zürich, Switzerland	bagheri@ieu.uzh.ch
Joke Bakker		University of Groningen, NL	joke.bakker@rug.nl
Mychal Bolton		East Tennessee State University, USA	bolton@goldmail.etsu.edu
Romain Bourget	T	LAREMA, France	bourget.romain@gmail.com
Mark Broom	T	City University London, UK	Mark.Broom@city.ac.uk
John Bryden	T	University of London, UK	john.bryden@rhul.ac.uk
Roland Byron	P	East Tennessee State University, US	roland@goldmail.etsu.edu
Sharon Cameron		East Tennessee State University, USA	zsmc70@goldmail.etsu.edu
Ruth Castillo Cajas		University of Groningen, NL	r.f.castillo.cajas@rug.nl
Loïc Chaumont	T	Université d'Angers, France	loic.chaumont@univ-angers.fr
Dan Cohen	T	Hebrew University of Jerusalem, Israel	dancohen@vms.huji.ac.il
Zoe Cook	T	University of York, UK	zc505@york.ac.uk
Stephen Cornell	T	University of Leeds, UK	s.j.cornell@leeds.ac.uk
Derek Crouther		East Tennessee State University, USA	crouther@goldmail.etsu.edu
Folkert de Boer		University of Utrecht , NL	fkdeboer@gmail.com
Monique de Jager	T	NIOO-KNAW, NL	m.dejager@nioo.knaw.nl
Harold de Vladar	T	IST, Austria	hpvladar@ist.ac.at
Cornelis Drost	T	IBERS, Aberystwyth University, UK	cjd09@aber.ac.uk
Fátima Drubi		University of Leiden, NL	drubi@cml.leidenuniv.nl
Xiaoguang Du	T	University of Groningen, NL	x.du@rug.nl
Alex Dumbrell		University of Essex, UK	adumbrell@essex.ac.uk
Francisco Encinas Viso	T	University of Groningen, NL	f.a.encinas.viso@rug.nl
Rampal Etienne	T	University of Groningen, NL	r.s.etienne@rug.nl
Tim Fawcett	T	University of Bristol, UK	tim.fawcett@cantab.net
Meghan Fitzgerald	T	University of Wisconsin Madison, USA	mrfitzgerald@wisc.edu
Lindsey Fox		East Tennessee State University, USA	foxlr1@goldmail.etsu.edu
Franz, Matthias	T,P	CRCESB Göttingen, DE	mfranz2@gwdg.de
Javier Gamarra		IGES/IBERS, Aberystwyth University, UK	jgg@aber.ac.uk
Atiyo Ghosh	T	University of Leiden, NL	ghosh@cml.leidenuniv.nl
Ava Gooding		East Tennessee State University, USA	zaeg10@goldmail.etsu.edu
Charlotte Hemelrijk	T	University of Groningen, NL	c.k.hemelrijk@rug.nl
Geerten Hengeveld	P	NIOO-KNAW, NL	g.hengeveld@nioo.knaw.nl
Andrew Higginson	T	University of Bristol, UK	a.d.higginson@bristol.ac.uk
Martin Hinsch		University of Groningen, NL	hinsch.martin@gmail.com
Paulien Hogeweg	K	University of Utrecht , NL	P.Hogeweg@bio.uu.nl
Oleksandr Ivanov	P	University of Groningen, NL	krystoferivanov@gmail.com

Aniek Ivens	T	University of Groningen, NL	A.B.F.Ivens@rug.nl
Thijs Janzen	P	University of Groningen, NL	t.janzen@rug.nl
Daniel Jones	T	Goldsmiths University of London, UK	d.jones@gold.ac.uk
Chris Klausmeier	K	Michigan State University, USA	klausme1@msu.edu
Andrea Kölzsch	T	NIOO-KNAW, NL	a.koelzsch@nioo.knaw.nl
Marek Kwiatkowski	T	ETH Zürich, EAWAG, Switzerland	marek.kwiatkowski@eawag.ch
Rebecca Leonard		East Tennessee State University, USA	leonarra@goldmail.etsu.edu
Simon Levin	K	Princeton University, USA	slevin@princeton.edu
Hannah Lewis	T	University of St. Andrews, UK	hml2@st-andrews.ac.uk
Nicola Lewis	P	University of Essex, UK	ndlewi@essex.ac.uk
Marjolein Lof	T	NIOO-KNAW, NL	m.lof@nioo.knaw.nl
Andri Manser		University of Zürich, Switzerland	andri.manser@ieu.uzh.ch
James Marshall	T	University of Sheffield, UK	james.marshall@sheffield.ac.uk
Luke McNally	T	Trinity College, Dublin, Ireland	mcnalll@tcd.ie
Carlos Melian	T	CEEB, EAWAG, Switzerland	carlos.melian@eawag.ch
Géza Meszéna	T	Eötvös University, Hungary	geza.meszena@elte.hu
Hans Metz	K	University of Leiden, NL	J.A.J.Metz@biology.leidenuniv.nl
Lucas Molleman	P	University of Groningen, NL	l.s.molleman@rug.nl
Carina Mugal	T	Uppsala University, Sweden	carina.mugal@ebc.uu.se
Stuart Natrass	P	University College London, UK	stuart.nattrass.09@ucl.ac.uk
Bastian Niebel	P	University of Groningen, NL	b.niebel@rug.nl
Etsuko Nonaka		University of Umeå, Sweden	etsuko.nonaka@gmail.com
Sally Otto	K	University of British Columbia, Canada	otto@zoology.ubc.ca
Ido Pen		University of Groningen, NL	i.r.pen@rug.nl
Jorge Peña	P	University of Lausanne, Switzerland	jorge.pena@unil.ch
Sofia Piltz	P	University of Oxford, UK	sofia.piltz@linacre.ox.ac.uk
Mario Pineda-Krch	T	Centre for Mathematical Biology, Canada	mpineda@math.ualberta.ca
Bob Planqué	T	VU University Amsterdam, NL	r.planque@vu.nl
Ivan Puga-Gonzalez	T	University of Groningen, NL	I.Puga-Gonzalez@rug.nl
Andrés Quiñones	P	University of Groningen, NL	a.q.quia.ones.paredes@student.rug.nl
David Ramsey	T	University of Limerick, Ireland	david.ramsey@UL.ie
Sean Rands		University of Bristol, UK	sean.rands@bristol.ac.uk
Daan Reid	T	Universty of Groningen, NL	osmosis@dds.nl
Luke Rendell	P	University of St. Andrews, UK	ler4@st-andrews.ac.uk
Chelsea Ross		East Tennessee State University, USA	zcrr23@goldmail.etsu.edu
Axel Rossberg	T	Queen's University of Belfast, UK	axel@rossberg.net
Jasper Ruifrok	T	Universty of Groningen, NL	j.l.ruifrok@gmail.com
Abdulquadri Salahdyin		University of Nigeria	salahdyinabdulquadri@yahoo.com
Sinha Somdatta	T	CCMB, India	sinha@ccmb.res.in
Peter Sozou	T	London School of Economics, UK	p.sozou@lse.ac.uk
Mark Stevenson	P	Queen Mary University of London, UK	m.stevenson@qmul.ac.uk
Jasmine Sutton		East Tennessee State University, USA	suttonjm@goldmail.etsu.edu
Corina Tarnita	K	Harvard University, USA	corina@math.harvard.edu
Sam Tazzyman	T	University College London, UK	s.tazzyman@ucl.ac.uk
Kirsten ten Tusscher	T,P	University of Utrecht, NL	K.H.W.J.tenTusscher@uu.nl
Pete Trimmer	T	University of Bristol, UK	pete.trimmer@gmail.com
Johan van de Koppel	T	NIOO-KNAW, NL	j.vandekoppel@nioo.knaw.nl
Femke van den Berg	T	Rothamsted Research, UK	Femke.vandenberg@bbsrc.ac.uk
Piet van den Berg		University of Groningen, NL	pieter.van.den.berg@rug.nl
Daniel van Denderen		IMARES Wageningen, NL	daniel.vandenderen@wur.nl

Joost van den Heuvel	T	University of Leiden, NL	j.van.den.heuvel@biology.leidenuniv.nl
Daniel van der Post	T	University of Groningen, NL	d.j.vanderpost@gmail.com
Sander van Doorn	T	University of Bern, Switzerland	vandoorn@iee.unibe.ch
Jordi van Gestel	P	University of Groningen, NL	J.van.Gestel@student.rug.nl
Jordan VanHoy		East Tennessee State University, USA	vanhoyjs@goldmail.etsu.edu
Ellen van Velzen	T	University of Groningen, NL	e.van.velzen@rug.nl
Severine Vuilleumier	T	University of Lausanne, Switzerland	severine.vuilleumier@unil.ch
Andreas Wagner	K	University of Zürich, Switzerland	aw@bioc.unizh.ch
Franjo Weissing	T	University of Groningen, NL	f.j.weissing@rug.nl
Lev Yampolsky	T	East Tennessee State University, USA	yampolsk@etsu.edu
Alexey Yanchukov	P	University of California, USA	yawa33@gmail.com
Jon Yearsly	T	University College Dublin, Ireland	jon.yearsley@ucd.ie
Guillermo Zampar	P	University of Groningen, NL	guillezampar@gmail.com
Chunyan Zhang		University of Groningen, NL	zhcy@pku.edu.cn
Jian Lei Zhang		University of Groningen, NL	jianleizhang@pku.edu.cn