Minisymposium - Game Theory in Ecology and Evolution
European Conference on Mathematical and Theoretical Biology 2014

Theoretical developments in evolution and ecology have undergone a sea change since the inception of evolutionary game theory in the early seventies. In combination with population genetics, this has enabled theoretical aspects of biological systems to be understood at the genotypic as well as the phenotypic level. This understanding has pervaded a plethora of fields from language evolution to cancer dynamics. This minisymposium focuses on recent mathematical and theoretical developments in evolutionary game theory in ecology and evolution.

Organizers

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Program Monday 16th June 2014

Session I **Chair: tba**

0900 Jacek Miękisz (miekisz@mimuw.edu.pl)
Time delays in stochastic models of evolutionary games

0925 Chris Cannings (C.Cannings@shef.ac.uk)
Combinatorial Aspects of Parker's model

0950 Vlastimil Kivan (vlastimil.krivan@gmail.com)
The optimal foraging game

Coffee Break (1015-1045)

Session II **Chair: tba**

1045 Jacob Johannsson (jacob.johansson@biol.lu.se)
Game theory and adaptation of reproductive phenology to climate change in birds with dominance hierarchies

1110 Torbjrn Lundh (torbjorn.lundh@chalmers.se)
Cross-feeding as a game

1135 Kristian Lindgren (kristian.lindgren@chalmers.se)
Evolutionary Exploration of the Finitely Repeated Prisoners Dilemma - The Effect of Out-of-Equilibrium Play

1200 Lars Bach (lbach@hum.au.dk)
tba

1225 Krzysztof Argasinski (argas1@wp.pl)
Natural selection under limited population growth. Replicator dynamics and eco-evolutionary feedback

1250 **Closing comments**

Abstracts

Jacek Miękisz

Time delays in stochastic models of evolutionary games

It is usually assumed that interactions between individuals take place instantaneously and their effects are immediate. In reality, all social and biological processes take certain amount of time. It is natural therefore to introduce time delays into evolutionary game models. We will discuss combined effects of stochasticity and time delays in various finite-population, discrete-time evolutionary games. A state of a population of individuals is stochastically stable if it appears with a high frequency in the limit of small stochastic perturbations of deterministic dynamics. We show the existence of a stochastically stable cycle in two-player games with a mixed evolutionarily stable strategy for any discrete time delay. The situation is much more complex in there-player games with two evolutionarily stable strategies, a mixed and a pure one. In particular, we show that if the basin of attraction of the mixed equilibrium is bigger than the one of the pure equilibrium, then there exists a critical time delay where the pure equilibrium becomes stochastically stable.

Bibliography

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J Miekisz and S Wesoowski, Stochasticity and time delays in evolutionary games, Dynamic Games and Applications 1: 440-448 (2011).

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Chris Cannings

Combinatorial Aspects of Parker's model

Individuals are located at the vertices of the (simple) graph $G = (V, E)$, and at time t play either 0 or 1. At time $(t + 1)$ an individual will play 0 if, and only if, more of their neighbours were playing 0 at time$t$ than were playing 1 at time t. This is the Majority Game, and we shall assume that all vertices have odd degree so that there is never equal numbers of 0s and 1s amongst neighbours. This game is a special case of a threshold game and so the system must converge to fixed point or to a two cycle. We shall explore features of the dynamics on some particular regular graphs, most importantly the hypercube. The Minority game is dual to this. At $(t + 1)$ an individual will play 0 if, and only if, more of their neighbours were playing 1 at time t than were playing 0 at time t. We shall briefly examine some of the consequences of having a mixture of majority players and minority players, when the dynamics is more complex than the homogeneous game. **Key Words:** majority/minority game, dynamics, thresholds, cycles.

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Vlastimil Kivan

The optimal foraging game

In a multi-prey environments, the optimal foraging theory predicts a foragers diet that encounters two or more prey types sequentially. The predictions are based on maximization of a generalized multi-prey Holling type II functional response. The results predict that the most profitable prey type will always be included in the predators diet. The other, less profitable prey types will either be included, or excluded from the diet. This result is known as the 0-1 rule of the optimal foraging theory. In my talk I will discuss how these results can be obtained in context of the game theory. In particular, I will discuss how a functional response can be derived using decision trees. Solutions of the foraging game are then sought in the form of an agent normal form. In particular, I provide some conditions under which the solution of the optimal foraging theory coincides with the Nash equilibrium of the foraging game. I will show examples where predators can encounter prey types simultaneously, or the predator requires a positive recognition time to identify the type of prey encountered.

R. Cressman, V. Krivan, J. S. Brown, J. Garay: Game-theoretic methods for functional response and optimal foraging behavior, Plos One, 2014.

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Torbjrn Lundh

Cross-feeding as a game

In many ecologies organism exchange of metabolites in a process known as cross-feeding, which leads to complex dependencies

on fitness. We have created an artificial ecology called Urdar (after the well where the norse universe, i.e. the ash tree Yggdrasil was growing) in order to study cross-feeding in a highly controlled experimental yet digital environment. We will discuss three questions in relation to this system: i) Is a cross-feeding ecology with a higher nutrient influx be more or less diverse? ii) Will a cross-feeding population converge towards an optimal configuration with respect to the overall productivity? iii) What can be said about the dynamics of three cross-feeding species if pairwise interactions are known?
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Jacob Johannsson
Game theory and adaptation of reproductive phenology to climate change in birds with dominance hierarchies
with Henrik G. Smith, and Niclas Jonzn
One of the most striking ecological responses to recent climate change is the shift in the timing of seasonal events (phenology) documented in a wide range of organisms. The adaptive value and the demographic consequences of these changes are often poorly known, however. We develop a game theory model to study adaptation of timing of reproduction in birds with social dominance hierarchies. Specifically, we consider resident birds with winter flocks where early-fledged juveniles obtain higher ranking because of prior residency advantages when flocks are formed. In the absence of competition birds should time their reproduction to maximize the availability of food suitable for rearing the offspring in the form insect larvae available only during a short period during spring. However, owing to the competitive advantages of early fledging, the evolutionarily stable strategy (ESS) is to let offspring hatch before the date that maximizes the availability of their food. We study the effects of environmental change on breeding population densities, ensuing selection pressures and long-term evolutionary equilibria in this system. We show that the ESS hatching date will advance with increasing winter survival and habitat productivity since these factors increases the pressure of the post-fledging competition. While much previous literature mainly links selection on reproductive phenology to changes in food peak dates, our model offers a conceptually new set of explanations for understanding phenological and demographic trends in a changing climate. Moreover these findings emphasize that treating phenology as an evolutionary game rather than an optimization problem fundamentally changes what is to be considered as an adaptive response to climate change.
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Lars Bach
tba
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Kristian Lindgren
Evolutionary Exploration of the Finitely Repeated Prisoners Dilemma - The Effect of Out-of-Equilibrium Play
The finitely repeated Prisoners Dilemma is a good illustration of the discrepancy between the strategic behaviour suggested by a game-theoretic analysis and the behaviour often observed among human players, where cooperation is maintained through most of the game. A game-theoretic reasoning based on backward induction eliminates strategies step by step until defection from the first round is the only remaining choice, reflecting the Nash equilibrium of the game. We investigate the Nash equilibrium solution for two different sets of strategies in an evolutionary context, using replicator-mutation dynamics. The first set consists of conditional cooperators, up to a certain round, while the second set in addition to these contains two strategy types that react differently on the first round action: The “Convincer strategies insist with two rounds of initial cooperation, trying to establish more cooperative play in the game, while the “Follower strategies, although being first round defectors, have the capability to respond to an invite in the first round. For both of these strategy sets, iterated elimination of strategies shows that the only Nash equilibria are given by defection from the first round. We show that the evolutionary dynamics of the first set is always characterised by a stable fixed point, corresponding to the Nash equilibrium, if the mutation rate is sufficiently small (but still positive). The second strategy set is numerically investigated, and we find that there are regions of parameter space where fixed points become unstable and the dynamics exhibits cycles of different strategy compositions. The results indicate that, even in the limit of very small mutation rate, the replicator-mutation dynamics does not necessarily bring the system with Convincers and Followers to the fixed point corresponding to the Nash equilibrium of the game. We also perform a detailed analysis of how the evolutionary behaviour depends on payoffs, game length, and mutation rate.
Reference:
Lindgren K, Verendel V. Evolutionary Exploration of the Finitely Repeated Prisoners Dilemma – The Effect of Out-of-Equilibrium Play. Games, 4(1):1-20, 2013.
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Krzysztof Argasinski

Natural selection under limited population growth. Replicator dynamics and eco-evolutionary feedback.

In this talk we discuss a new approach to the derivation of population dynamic models called “event based modelling,” which relies on the assumption that the trajectory of the process is the aggregated outcome of individual interactions (i.e. “atomic” events) occurring with respective rates. Thus, the methodology resembles that of chemical kinetics where the interaction rate is the analogue of the reaction rate. In this approach, instead single abstract fitness function, describing growth rate, there are two separate mortality and fertility payoff functions. An important aspect of the presented framework is the explicit incorporation of growth limitations. The regulation of the population size acts through feedback driven by density dependent juvenile mortality. It was shown that at the population size equilibrium, newborns form a pool of candidates from which survivors who will replace dead adults at their nest sites will be drawn. Thus fertility payoffs can be interpreted as the entries of a nest site lottery mechanism. The new approach emphasizes the role of the turnover of individuals. In this case the stable population size is a dynamic equilibrium between different mortality and fecundity factors instead of an arbitrary fixed carrying capacity. This mechanism can be regarded as an example of eco-evolutionary feedback. This seriously alters the predictions of game-theoretic models in comparison to models with unlimited growth. In this case there can be for example two stable manifolds: one for the frequency dynamics and a second for the population size. The global stationary points are intersections of those manifolds. For example in the Hawk-Dove Game, a pure Hawk population can become evolutionarily stable in addition to the stable mixed equilibrium known from the classical theory. This is caused by the fact that the payoff structure is not constant. The most intriguing result is that under the impact of eco-evolutionary feedback, an apparently unstable invasion barrier between two pure-strategy stable equilibria can become stable at the intersection with the stable density manifold.

ARGASINSKI, K.; BROOM, M. Ecological theatre and the evolutionary game: how environmental and demographic factors determine payoffs in evolutionary games. Journal of Mathematical Biology, 2012, 1-28.

ARGASINSKI, K.; BROOM, M. The nest site lottery: how selectively neutral density dependent growth suppression induces frequency dependent selection .Theoretical Population Biology 90 82-90, 2013

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