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Game theory and evolutionary ecology

Evolutionary Games & Population Dynamics

by J. Hofbauer and K. Sigmund

Cambridge University Press, 1998.
£50.00 hbk, £16.95 pbk
(xxvii + 323 pages)
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Game Theory & Animal Behaviour

edited by L.A. Dugatkin and H.K. Reeve

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The liaison between game theory and evolutionary ecology has become a serious and intimate affair during the past few years. The book by Hofbauer and Sigmund will convince even the sceptical of this liaison. *Evolutionary Games & Population Dynamics*, a thorough revision and extension of the successful 1988 textbook entitled *Theory of Evolution and Dynamical Systems* by the same authors, makes the conceptual and the mathematical links between these two disciplines obvious. Perhaps the most striking evidence is that the dominant model types of evolutionary game dynamics (replicator equations) and of population dynamics (Lotka–Volterra equations) are, in many instances, mathematically isomorphic. Behind their mathematical equivalence lies a deep, substantial homology between replicator dynamics and population dynamics, namely the fundamental, 'like begets like' assumption that they share. From the modeller's perspective, it makes little difference whether the differential properties of the multiplying entities are called strategies or species: the common essence of the replicator-dynamic and the population-dynamic approach is that a set of populations (each assigned a specific heritable trait) compete, or cooperate, for a set of limiting resources. Resources are sometimes explicit, but more often they are implicit, components of the models.

Before leading the unsuspecting reader to the wrong conclusion that there are two identical methodologies, one of which is superfluous, let me stress the difference between the two sets of models that is perhaps the most important. The usual state variable of game-theoretical models in general, and replicator dynamics in particular, is a vector of relative replicator frequencies that add up to one for the whole system. This implies a complete disregard of information about absolute population sizes on the one hand, and the relative frequency dependence of the interactions among strategies on the other. From the biologist's viewpoint, the latter is a fundamental difference compared with the usual models of ecological interactions. The state variables of Lotka–Volterra models are density vectors that are not constrained on the unit simplex: each density can take any non-negative real value. Consequently, ecological interactions are assumed to be density dependent (i.e. it is not only the relative but also the absolute size of a population that determines the intensity of its interactions). The cost of this additional detail is one of a methodological nature: density dependence adds an extra dimension to the corresponding system of differential equations, which can make certain analytical techniques difficult to apply. Frequency and density dependence can be assumed even within the same model, but at the cost of even more mathematical complications. This means that numerical simulation is the only accessible tool for model analysis[1].

Both from the mathematical and from the biological standpoint, a key concept of *Evolutionary Games & Population Dynamics* is permanence, a new stability property for dynamic systems. Roughly speaking, it covers perturbation resistance close to the margins of the state space, which is obviously an important property in game dynamics, given that the invasions of new strategies start from states near the boundary, with a low abundance of invaders. Mathematically, a system is permanent if the boundary of its state space repels towards the interior. In biological terms, this means that an existing combination of strategies is stable against sufficiently small and sufficiently rare disturbances. Such disturbances do not drive extant strategies to extinction. This concept of permanence is also applicable, with the necessary changes, to strictly ecological (i.e. density-dependent) models.

Embedding population genetics into population-dynamical models has always been a notoriously difficult problem of mathematical biology. A large part of the difficulty arises from the fact that population dynamics mostly applies density-dependent models, whereas population genetics has always been interested in relative allele frequencies. A more natural link between game dynamics and population genetics can be established on the common platform of relative frequency dependence. Promising and interesting steps taken in this direction have been explained in a separate section of the book.

Evolutionary Games & Population Dynamics is an excellent textbook on dynamic systems applied in ecology and evolutionary biology and is written in a clear, elegant and enjoyable style both in the text and in the mathematical sections. Hundreds of exercises and a thorough further-reading list help the reader to understand the concepts and theorems presented. In a certain sense, this is an interdisciplinary volume touching upon many different fields of theoretical biology, yet it is very far from being a superficial overview of everything. Reading the book provides an enjoyable and challenging intellectual experience. In the section entitled 'About this book', the authors themselves suggest certain parts for game theorists to read, other parts for mathematical ecologists and still other parts for evolutionary geneticists. It turns out that they do not recommend anybody to read the entire book. But let me suggest that you do. It is definitely worth the effort.

Game Theory & Animal Behaviour is an edited volume loosely based on talks covering a diverse set of subjects that were presented by the authors at the 1995 symposium of the National Animal Behavior Society, USA. The scope of the book is accordingly wide: the topics range from pure theory aimed at a concise summary of the basics of game theory and a review of the links between the models of game theory, evolutionary optimality theory and quantitative genetics, to game theory applied to hypothetical

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or actual animal conflicts in social foraging (among other topics), and a verbal consideration of the applicability of game theory to important aspects of human behaviour such as social norms.

The common framework for the selection of papers is classic evolutionary game theory – perhaps one of the most influential paradigms of the century – initiated by Von Neumann and Morgenstern[2], Nash[3] and Maynard Smith[4]. This equilibrium-oriented approach proves to be as useful as expected from past and recent developments in the discipline. Realistic, 'field-motivated' situations of the many different types of animal conflict covered in the book fit nicely into elegant, mathematically simple models. Most of the authors compare model predictions with sound empirical evidence – although the amount of evidence and taxonomic diversity discussed in each chapter are quite different. One has the impression that empirical work keeps pace with game-theoretical modelling in the study of animal behaviour, which is an enviable state of affairs compared with some other disciplines of theoretical biology.

The general applicability of classic evolutionary game theory to problems far from those of animal conflicts is a recurrent claim of publications on the subject. The usual list of disciplines taking advantage of such secondary applications includes economics, social science and even the humanities. Interestingly, it is rarely stated that evolutionary game theory has much to say to other fields of population biology. For example, within-community multispecies coevolution of plants calls for a game-theoretic approach, with growth forms and/or dispersal techniques considered as strategies, and possible stable equilibria representing evolutionarily stable coalitions. There are good reasons to expect that game theory will help us explain plant 'behaviour' and, on that basis, certain aspects of community diversity. This would be yet another link in the promising relationship between game theory and evolutionary ecology.

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Rivers of life

Restoring Life in Running Waters: Better Biological Monitoring

by J.R. Karr and E.W. Chu

Island Press, 1998.
$29.95 pbk (xiv + 206 pages)
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The concept of ecological services has been warmly embraced as a pragmatic justification for the conservation of biological diversity[1,2]. Experiments reveal that more diverse terrestrial communities are better at fixing carbon dioxide (CO_2) or show increased resilience in the face of drought or other perturbations[3,4]. Unfortunately, the generality of these findings is unclear because the experimental communities involved are, of necessity, small or artificially contrived, and the challenges of extrapolating the results, to rain forests for example, are considerable. In freshwater systems, by contrast, the logic for conservation is incontrovertible. Clean water is fundamental to life. Healthy river systems deliver not just a water supply, but also fish, power generation, transport, recreation and cultural identity. The demand for these services will intensify as populations grow and countries develop, and it is widely predicted that the battles of the 21st century will be waged over water resources rather than oil or territory.

Biologists are faced with the challenge of monitoring the wellbeing of freshwater habitats. Happily, the task is relatively straightforward because the status of the living organisms found there is the best indicator of condition. Even more propitiously, the preservation or restoration of natural systems, and the associated biological diversity, emerges as the most effective way of guarding freshwater resources. With this impetus, it is not surprising that considerable effort has been devoted to creating measures that encapsulate biological quality in a single figure. Karr and Chu review this approach and make a strong case for the adoption of multimetric biological indices in river assessment and management. Although their book is focused on the United States, much of the discussion is of wider relevance.

Multimetric measures are used to generate an index of biological integrity (IBI). This is a composite of around eight to 12 metrics, or variables, each chosen to reflect some aspect of the system's biological health. The metrics span a range of attributes, including the richness of specified taxa, trophic structure, such as the relative abundance of predators, and rates of disease or malformation in target species. They need not be independent. Indeed, a typical IBI, such as one used in the midwestern USA, includes the total number of fish species as metrics, as well as the richness of separate taxonomic groupings, such as darters and sunfish. Each metric is ranked from one to five, with five being the value expected for a pristine habitat. The metrics are summed to produce the final index, which is then used to compare and assess sites.

Ecologists are often suspicious of measures that pool disparate variables. Experience with diversity statistics, such as the Shannon index, has for instance revealed how an assumed virtue – in this case, the integration of richness and evenness scores – can thwart interpretation. Nonetheless, the authors discuss 37 premises (e.g. 'statistical decision rules are no substitute for biological judgement') on which the case for multimetric measures is based, and criticize seven 'myths' (e.g. 'the sensitivity of multimetric measures is unknown') that have been advanced against them. Karr and Chu also note that multimetric indices are statistically versatile and can be analysed with familiar techniques, such as ANOVA or regression, and that the precision of sampling protocols can be estimated in conventional ways. Moreover, IBIs are not just confined to rivers. The book lists a variety of environments, including lakes and coastal and marine systems, in which they have been successfully applied.

Karr and Chu argue that multimetric measures are easily comprehensible and draw an analogy with economic indicators such as the Dow Jones industrial average. But whereas the Dow Jones generates a single measure of the economic status of one country, IBIs are faced with a broader task. Pristine freshwater habitats can vary markedly from place to place and estimates of species richness (a central component of many IBIs) are not an infallible guide to ecological quality. Headwater streams, for example, typically support fewer species than large rivers. The authors address this concern, maintain that multimetric measures can be wide-ranging and cite, as evidence, a fish IBI that successfully classified sites in six US regions ranging from Chicago to Arkansas. However, they also recognize that the proper classification of sites, so that like is compared with like, is the key to a successful IBI.

There is no doubt that IBIs have been a valuable tool in the monitoring and conservation of American rivers and Karr and Chu provide a compelling case for their universal adoption. Given the importance of benchmark data in the selection of metrics and appropriate deployment of IBIs, it remains to be seen if they can fulfil their promise in diverse, and increasingly threatened, tropical rivers for which we have depressingly little biological information.

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