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)
ISBN 1 55963 674 2

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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The scourge of society

Parasites in Social Insects

by Paul Schmid-Hempel

Princeton University Press, Monographs in Behavior and Ecology, 1999.
£60.00 hbk, £24.95 pbk
(xi + 409 pages)
ISBN 0 691 05923 3 / 0 691 05924 1

One of us studies parasites, and the other social insects. There is a large gulf between our two disciplines, a gulf that is bridged admirably by Paul Schmid-Hempel in an ambitious new book. *Parasites in Social Insects* synthesizes an eclectic and dispersed literature with such thoroughness and near-passion that, barring a global rush to study these parasites, it should stand for years to come as an authoritative reference. It has two great strengths.

First of all, it is undeniably thorough. With 55 pages of references, a glossary, and a delightfully comprehensive appendix entitled simply 'The Parasites of Social Insects', this is not a volume for the faint of heart. The first two chapters are devoted to introducing the main players – social insects and parasites. The following six chapters examine the interaction of these players from a variety of perspectives, from colony organization and parasitism to social evolution itself. Interspersed among these chapters are a host of tables, figures and boxes for detailed treatment of special topics. If there is anything you want to know about the parasites of social insects, this is the place to look.

Second, Schmid-Hempel identifies a wealth of unplumbed research topics. He does so with such enthusiasm that there might well be a global rush to work on the parasites of social insects. Many of the lacunae he identifies mirror those in our understanding of host–parasite biology in general. Pure survey and/or demographic data are sorely lacking for many systems. We know little about the regulatory ability of parasites for host populations, little about the interplay of most host and parasite genetic systems, and little about the influence and extent of multiple infections.

The very fact that the hosts in question are social allows for novel treatment of traditional questions in parasitology and sociobiology, to the benefit of both areas. Although we both found the book to be important, we disagreed on which sections we found most interesting and innovative. Parasitologists will be intrigued by the implications of social structure for interactions between hosts and parasites. For instance, the action of parasites on social insects can be viewed at two levels – that of the infected individual and that of the invaded colony. Transmission among colonies might favor aspects of parasite evolution that differ from those favored by transmission within colonies. Furthermore, parasite population dynamics are complicated by differential mortality rates of individuals versus colonies. Individual insects might show immunity to parasites, and entire colonies can display behavioral responses to cope with infections. Colony size itself is an important variable to include, and colony organization (division and labor and deployment of the worker force) can either enhance or retard transmission.

Likewise, some concepts that are familiar to parasitologists might intrigue social insect biologists. For instance, island biogeographical theory has been applied to relationships between host ranges and parasite richness[1]; Schmid-Hempel notes that large colonies with large foraging potential might have a higher risk of encountering novel parasites. Many birds and mammals leave nests and foraging areas in the presence of parasites[2,3]; Schmid-Hempel suggests that parasites might motivate nest relocation in social insects.

The book is not perfect. It is marred by a surprising number of typos and minor factual errors (e.g. incorrect descriptions of insect species and incorrect references to parasite biology), and we disagree with some conceptual treatments (e.g. the confounding of virulence and parasite reproduction). Such quibbles aside, Schmid-Hempel has produced an admirable book that is at once a remarkable work of scholarship and a source of inspiration for future study.

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