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Book Reviews

Parasites in Social Insects. By P. SCHMID-HEMPEL. Princeton, New Jersey: Princeton University Press (1998). Pp. xi+409. Price $85.00 hardback, $35.00 paperback.

It is the push and pull of natural selection between hosts and parasites that makes the study of their interactions rewarding and instructive to evolutionary biologists, and increasingly to students of animal behaviour (Hart 1990; Poulin 1994). This evolutionary struggle is especially salient in complex societies, where an adaptive level of biological organization above that of the individual must interact with parasites and pathogens.

A reading of Schmid-Hempel's book suggests that the study of parasites and pathogens of social insects might be considered, with apologies to Tom Lehrer, as a specialization on diseases of the rich. From the perspective of natural enemies, insect societies have a lot to offer. Homeostatically controlled nest environments (often warm and moist), copious food stores, and large populations of hosts coalesce in a confined space. These are but a few among the many resources that insect societies offer to assorted moochers and hangers-on. However, the rich are forced (and can often afford) to defend themselves against those who would rob from their larders, and social insect defences against parasites can be wielded at group as well as individual levels. Furthermore, the insect colony is a complex and dynamic environment, comprising individuals at different developmental stages, with diverse genotypes, sometimes from many morphological castes, and frequently with complex age-related changes in adult behaviour. Schmid-Hempel employs the factory–fortress metaphor for insect colonies to good effect, exploring the ways that colonies and their members can evolve to resist parasites. The book surveys what is known about the range of outcomes of social insect/parasite conflicts.

However, notwithstanding a few well-studied, even classic, examples of parasite interactions with social insects (*Dicroceolium* spp. flukes' manipulation of the behaviour of their ant intermediate hosts should be familiar to anyone who has studied parasitology), Schmid-Hempel's review emphasizes that our understanding of social insects' host–parasite relationships is poorly developed. In part this is due to the complex nature of host–parasite interactions, complexity that is amplified by adding the society as a level of biological organization relevant to both players. At the opening of chapter 2, 'The Parasites and their Biology', Schmid-Hempel does not even present a clear definition of the term parasite, rightly pointing out that detrimental (i.e. negative fitness) effects of symbionts on hosts may be minor, transient and (in many cases) dependent on social and ecological context. To encourage breadth of comparison, the author hedges on the side of considering symbionts that may be parasites, even if negative effects on host fitness have not been demonstrated.

The book comprises eight chapters. The first three chapters are largely descriptive, presenting overviews (in order) of the natural and life histories of social insect hosts, their parasites and modes of infection. Schmid-Hempel's stated goal for the remaining chapters (4–8) is to synthesize what is known about social insect host/parasite biology, and thereby to generate testable predictions to be addressed in future research. The book has a number of features that make it a highly useful reference, and that reflect the care and effort of the author. It includes a glossary and indexes to theoretical subjects, host taxonomy and parasite taxonomy. The chapters are enriched with boxes that present mathematical models and their main predictions in detail, often with graphical illustration of results. I especially enjoyed the many nonintuitive predictions from the models of population dynamics (chapter 6), a topic that has received little attention from social insect biologists (Jeanne & Davidson 1984). Most impressive, however, is Appendix 2, which is a taxonomically organized table summarizing known cases of parasites that infect social insects, with brief remarks on notable features of most of the interactions. Perusal of this table drives home the main message of the book: that parasites can impact insect societies in diverse and important ways, and should be considered as a potent selective force that shapes insect colonies.

Chapters 4–8 contain a wealth of ideas for further investigation. Schmid-Hempel argues convincingly that parasites are an alternative selection pressure that can affect many well-studied adaptations of insect societies. For example, parasites can select for changes in colony developmental trajectories (chapter 6), host energy allocation (chapter 7), kin recognition (chapter 8) and even the evolution of eusociality itself (chapter 8; O'Donnell 1997).

The author also points out that much of our knowledge of parasites of social insects is based on correlational studies, and is heavily biased towards a few host species of economic and/or political importance, for example, honeybees (*Apis*) and fire ants (*Solenopsis*). This book should serve as an inspiration for increased effort devoted to experimental analysis on a diversity of host and parasite taxa (Table 2 suggests a panoply of possible subjects). In many cases, the experimental manipulations will not be straightforward, given the complexities of host–parasite interactions. For example, Schmid-Hempel describes numerous cases where infection of hosts requires specific points of entry by the parasite into the body, such that simply inoculating colonies with parasites may not suffice to produce infection. Even simple measures of parasite epidemiology may not yield straightforwad interpretations: for example, repeated host population surveys for infection rate (parasite prevalence) will not reliably indicate the dynamics of an epidemic, which can be modelled only following measurements of parasite transmission among colonies and of host colony growth and longevity. The book makes clear, however, that as study systems amenable to

manipulation are developed, there is every reason to expect ample reward for research effort.

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Maternal Effects as Adaptations. Edited by TIMOTHY A. MOUSSEAU & CHARLES W. FOX. New York: Oxford University Press (1998). Pp. xiv+375. Price $65.00.

Twenty years after the spandrels of San Marco, it is possible again to talk about adaptation (and adaptationism), albeit in a clearly more sophisticated way than previously (e.g. Rose & Lauder 1996). The volume edited by Mousseau & Fox is concerned with maternal adaptations, those mechanisms that mothers employ to enhance the fitness of their offspring; with maternal effects, parents contribute more than genes to the next generation. These mechanisms can accelerate, deter or sometimes reverse other responses to selection and can have profound effects of population dynamics and our understanding of evolutionary processes. Indeed, simply recognizing that maternal effects exist means that we need to consider selective events across two generations. More specifically, a maternal effect occurs if the phenotype of an individual is determined not only by its own genotype and environment, but also by the phenotype or environment of the mother. In the preface, Mousseau & Fox note that in the past maternal effects were usually treated as environmental noise! But variation is not noise, and this volume is an excellent exposition of the role of maternal effects in maintaining phenotypic variation.

The volume is organized into four parts: (1) recent theoretical developments; (2) assessment and measurement of maternal effects; (3) reviews of maternal effects across taxa; and (4) case studies of the adaptive significance of maternal effects. Each part begins with a precis by the editors, providing an overview and organizational framework for the papers that follow.

The theoretical section includes papers on the evolutionary genetics of maternal effects, the interaction of social selection, sexual selection and maternal effects, the role of maternal effects in population dynamics, and the discussion of oviposition behaviour as maternal effects. There are a number of important messages from these chapters. When maternal effects are present, evolutionary processes cannot be partitioned into selection within versus between generations. The evolution of maternal effects involves selection among families. Maternal effects, relating offspring quality to per capita reproduction, can lead to oscillations in population dynamics (one of my favourite chapters, in part because of the simplicity of the model and the profundity of the consequences). Maternal behaviour that affects the environment of the offspring, such as egg-laying behaviour in parasitoids or butterflies, is as much a maternal effect as egg size or yolk allocation.

The second part of the book contains three excellent chapters that provide a guide for future empirical studies on the adaptive significance of maternal effects. The quantitative measurement and assessment of maternal effects present challenges in statistical analysis and experimental design. To some extent, recognition of maternal effects requires a change in the way that we think about parental contributions to offspring. That is, maternal effects are explicitly cross-generational and for design and analysis of experiments need to be viewed as an environmental (rather than a genetic) component of offspring fitness, even if the source of the component arises solely from the parent's genetic expression.

The last two parts of the book examine the specifics of maternal effects. The survey in the third part of the book is exciting, partly because it focuses on so many interesting organisms and partly because we see the ubiquity of maternal effects. These have been observed in a variety of plants, many species of birds, over 70 species of insects, and 20 species of fish, along with (of course) mammals. My own favourite topics, the oviposition behaviour of insects and life history variation in fish, are well represented. In both cases, we see the 'classical' maternal effect that there is a generally positive correlation between maternal size, egg size and offspring size and a generally positive correlation between egg size and survival. In birds, maternal effects can provide an explanation for the observation of a decline in clutch size as laying date increases. The case studies in the last part of the book include the maternal control of diapause in the flesh fly *Sarcophaga bullata*, maternal effects in side-blotched lizards, *Uta stansburiana*, environmental sex determination in the diamond back turtle, *Malaclemys terrapin* (where a mother places her egg determines whether that offspring will be female or male, possibly the ultimate maternal effect), and density-mediated maternal effects in the wild radish, *Raphanus sativus*.

Like wealth, maternal effects are inherited but not heritable; but also like wealth, they can be very important to the success of offspring. They affect the development, behaviour and life history of individuals, the interactions between individuals, and the population dynamics of species. They blur the distinction between genetic and environmental components of phenotypic variation and present a range of challenges from conceptual formulation to experimental design and assessment. But, to paraphrase Feller (1971), challenges are not overcome by ignoring them. This excellent volume will allow us both to face the challenges raised by maternal effects and to overcome these challenges, into an even more advanced understanding of adaptation.

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Cognitive Ecology: The Evolutionary Ecology of Information Processing and Decision Making. Edited by REUVEN DUKAS. Chicago: University of Chicago Press (1998). Pp. viii+420. Price $30.00 paperback.

The study of cognition has long held a central position in research on animal behaviour. Until recently, this line of research has focused on the neuronal processes that underlie the acquisition and manipulation of information. However, it is becoming increasingly clear that, like morphological, physiological, behavioural and life history characteristics, animal cognition should be seen as a biological feature that has been shaped by natural selection. In *Cognitive Ecology*, Dukas and several contributors advocate such an approach to animal cognition. The book presents many recent findings and re-examines some earlier hypotheses in animal cognition. It demonstrates how certain constraints imposed on nervous systems limit or bias animal behaviour. By putting complex behaviours into an ecological context and integrating knowledge on cognitive constraints and processes, *Cognitive Ecology* lays the foundation for a new field of study at the intersection of behavioural ecology and cognitive psychology. Ten chapters, written by expert contributors, review contemporary case studies and theoretical models.

The necessary first step of information processing is the gathering of sensory cues from one's environment. Enquist & Arak discuss the influence of receiver perceptual systems (and their constraints) on the evolution of signal form. Although one of the longest chapters in the book, it is enjoyable to read. The results of studies using evolving artificial neural networks are well integrated with discussion of theories on the evolution of signalling systems. Even the 'aesthetic sense' in humans is discussed. The authors show that perceptual mechanisms can be biased, and that such biases can drive signal evolution.

The focus of the book then moves on to cognitive constraints on information processing and their effects on animal behaviour. Dukas reviews the results of recent neurobiological and psychological studies about cognitive constraints to assess their ecological relevance for different behaviours of animals. Dukas convincingly demonstrates the importance of cognitive capacities for behaviours in many species. Such capacities were often left unconsidered in former investigations. We agree with Dukas that field experiments are necessary to test whether constraints identified in the laboratory actually matter in a more natural context, and whether they ultimately affect fitness.

In a chapter on the evolutionary ecology of learning, Dukas presents learning as a specific, complex type of phenotypic plasticity that allows an animal to alter its subsequent responses to certain stimuli. The evolution of learning is strongly affected by life history traits, such as foraging strategy, predation risk, mating behaviour and sociality. Dukas suggests that, in general, rich learning capacities appear to be associated with more complex ways of life. He also points out a lack of comparative phylogenetic studies on this topic, which are necessary for a better understanding of the evolution of learning.

In a detailed and well-presented case study on song sparrows, *Melospiza melodia*, Beecher et al. integrate proximate cognitive mechanisms of song acquisition and repertoire with field data on the function and adaptive significance of song. By showing how young birds decide which songs to adopt and how to combine song elements, the authors present interesting examples of well-studied complex cognitive capacities. Beecher et al. discuss differences between laboratory studies and results obtained in the field, and attribute these differences to the difficulty of simulating key ecological factors of the birds in the laboratory. Thus they urge that future studies on the topic be done predominantly in the field. Meanwhile, Hughes et al. (1998) have described a different free-living population of song sparrows that behaves very much like Beecher's birds do in the laboratory. These differences nicely demonstrate the variability of behaviour in different populations. It may well be that laboratory studies can still contribute important information to knowledge of song communication and song learning.

Many animal activities require spatial orientation. Two chapters deal with the adaptive importance of spatial orientation mechanisms. In the first such chapter, Dyer examines the prospects for a cognitive ecology of spatial orientation. Several case studies are discussed in detail, including path integration by insects, compass orientation in insects and birds, and landmark learning by insects. A point that reappears throughout the chapter is the question of innate versus learned navigation strategies and how, for example, specific temporal changes in environmental conditions favour the evolution or use of one or the other strategy. A second emphasis in this chapter is on the biological and physical constraints that influence the course and the outcome of selection on spatial orientation mechanisms. The question of how (if at all) brain size is a constraint for certain cognitive tasks is highlighted as a major area of future research.

With a review of neurophysiological experiments (such as hippocampus lesions and electrophysiological recordings), Sherry introduces the mechanisms of spatial memory in vertebrates. He elaborates on numerous examples for the importance of spatial memory, explains different types of spatial memory, and presents interesting results concerning the importance of hippocampus size in this context. Although knowledge about mechanisms of spatial memory is still fairly scarce, the correlations between particular behaviours, ecology of the species and hippocampus size illustrates the power of the integrative approach of cognitive ecology.

Animals must not only evaluate information about food location. They must also assess its quality, which is difficult because there is often wide variance around the mean quality of a food type. The chapter about risk-sensitive foraging by Bateson & Kacelnik stands out as one of the best for its clarity in writing, precision in use of terms and the careful and detailed introduction to some of the models currently debated in foraging theory. The chapter is theoretical, sometimes maybe too much so, and it gives good insight into the depth, breadth and complexity of what is known about behavioural phenomena and their possible explanations in foraging animals. The authors review extensive empirical evidence for animal sensitivity to variance and discuss factors that influence whether an animal should be risk averse or risk

prone. They convince the reader of the usefulness of a mathematical characterization of biological phenomena and how this approach can yield testable hypotheses. The need for a fusion of functional and mechanistic approaches is especially emphasized.

Foraging behaviour is influenced not only by environmental risks. It is also strongly constrained by time or energy limitations of the forager, and by the need to avoid predation. Ydenberg examines models of foraging and antipredator behaviour. He shows that, 30 years after its emergence, foraging theory can still expand our understanding of decision mechanisms. Variants of decision making are introduced, and discussed in the two different foraging contexts of provisioning and feeding. Using intriguing case studies, the author describes different foraging strategies (efficiency maximizing versus rate maximizing) and how the choice of strategy can be influenced by energy or time limitations. The analysis of the interplay between hard-wired and learned behaviour, and the analysis of information use in foraging decisions, are likely to be central aspects of future research in the new discipline of cognitive ecology.

Information acquisition and information use are also important factors in partner choice. In Dugatkin & Sih's chapter, the importance of selecting the right partners in contexts other than mating is emphasized. The chapter provides a good introduction to the field. It reviews the current literature on partner choice in different contexts and maintains the right balance between discussion of theories and concrete examples.

In the introduction to his book, Dukas defines the main goal of cognitive ecology as the integration of 'ultimate evolutionary and ecological thinking with knowledge of proximate mechanisms'. Most chapters of the book live up to this goal, but all contributions have a strong emphasis on behavioural ecology. The link to the cognitive/mechanistic perspective appears to be somewhat artificial in some chapters. Even though the book is subtitled 'The Evolutionary Ecology of Information Processing and Decision Making', and most of the authors strongly emphasize the evolutionary context, it is clear that the understanding of the evolutionary forces that have shaped the information-processing mechanisms underlying cognitive abilities is still very poor. One major goal of the new field of cognitive ecology will be to elucidate these forces.

We found *Cognitive Ecology* enjoyable to read. The chapters are well organized, of high quality and easily intelligible. The book offers a readily accessible overview that highlights many promising areas of research. The authors unify findings of previous research and point out numerous unanswered questions. This and the critical review of different experimental approaches and existing hypotheses makes the book stimulating reading, especially for graduate students like ourselves, but surely also for senior scientists in the fields of both evolutionary ecology and cognitive psychology. *Cognitive Ecology* advocates a new and integrative approach to questions that have been studied by generations of scientists. Obviously, many open areas for future research emerge when cognitive and ecological approaches are integrated. Such an integrative approach ultimately must prevail if modern biology is to achieve a truly synthetic understanding of animal cognition.

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Attitudes to Animals. Views in Animal Welfare. Edited by FRANCINE L. DOLINS. Cambridge: Cambridge University Press (1999). Pp. x+262. Price £40.00 hardback, £14.95 paperback.

Francine Dolins describes the aim of the book as 'to provide a foundation from which to judge in making ethical choices regarding animals', which is largely achieved. However, the degree of complexity, ease of reading and enjoyment differ between chapters. With some chapters, a prior knowledge of the subject is important, in order to understand and appreciate the discussion fully. There is no indication of the readership, but I would suggest that it is most relevant to those involved in the use of animals for teaching or research.

The first part of the book, on attitudes to animals, starts with an introduction by Dolins. Phyllis Passariello than discusses the influence of totemism on human attitudes to animals; some knowledge of the social sciences such as anthropology would help the reader to understand some of the terminology and concepts in this chapter. James Serpell discusses the ambivalence in attitudes between farmers and scientists to animals under their charge. Interviews showed that both farmers and scientists justify their involvement with animals in terms of providing a service to the general public (e.g. supplying the consumer with food) and in some cases claim high moral ground, for example searching for miracle cures for diseases. Distancing techniques such as the use of euphemisms were apparent in both groups, which are considerd to be strategies to avoid becoming attached to their animals. Amongst scientists, 'denial through distancing' was more common in those involved in invasive rather than noninvasive procedures.

In part II, on animal awareness, Françoise Wemelsfelder discusses the arguments on the use of subjectivity ('first-person perspective'), as a more relevant index of assessing animal suffering than the current mechanistic measures ('third-person perspective'). The discussion extends into the interpretation of abnormal behaviour and conscious awareness. These themes are central to the book and are covered from different perspectives elsewhere. Susan Healy & Martin Tovée review research on the effects of social and physical environments on sensory development. The nature of the topic necessitated a discussion of neurophysiological functions, which some may find difficult to follow; diagrams, for example to illustrate the development of the visual system, would have been helpful to the reader. The concept and evaluation of psychological well-being is addressed by Robert Young. In particular, he compares behavioural needs with behavioural void and debates the appropriateness of different

methods of assessment such as cost–benefit analysis, operant testing and behavioural resilience. Overall, he suggests that welfare requirements may be determined by the complexity of the species: 'simpler' species (e.g. birds) may suffer if their environment does not facilitate fixed-action behaviours; in contrast, complex species (e.g. mammals) suffer from not being able to satisfy the behavioural void. James King describes research on personality and happiness ('subjective well-being') in chimpanzees. There are 4505 descriptors of human personality, which have been condensed into five main traits, known as 'the Big Five'. Research has shown that these criteria can be reliably applied to chimpanzees and that personality may be a more important determinant of subjective well-being than external environment. The main focus of Richard Byrne's chapter is on the ability of nonhuman primates to anticipate future suffering, hypothesizing that if animals demonstrate the ability to anticipate events then they will have a greater capacity to experience suffering.

As an introduction to part III on animal welfare, Donald Broom discusses the semantics of the concept and definitions of animal welfare and related issues such as feelings and stress. David Shepherdson compares different components of environmental enrichment such as pyschological versus physical space and naturalistic versus artificial enrichment. It is an interesting chapter, acknowledging the radical effect that environmental enrichment can have not only on animal welfare but also on the ethos of zoos. In the last chapter of this section, Mary Midgley presents the arguments for and against animal rights and refers to the merits of compromise and complete revolution or abolition of welfare-unfriendly systems.

In part IV on research and education, Andrew Petto & Karla Russell's chapter on humane education considers the ethics of using animals for educational purposes. Petto & Russell highlight concepts such as 'moral ecology' which is a code of practice for teachers and their students to discuss the ethics of using animals for practical teaching classes. 'Minding animals' by Patricia Hindley gives a fascinating insight into the importance of animals for cognition and development of empathy and social skills in young children. Comparisons are made between human and animal consciousness. In a chapter on alternatives to using animals in education, David Dewhurst reviews the current extent of animal use in teaching in the U.K., and whether the timing and use of dissections and experiments on animals for educational purposes help to improve learning. He presents a range of alternatives to traditional dissections and experiments. Henk Verhoog questions the foundation of scientific methodology, and its impact on the attitude of teachers and researchers towards the use of animals. In the natural sciences, there is a series of similar dichotomies which differentiate between subject(ive) and object(ive), where only the latter is considered to be valid by the scientific community, whereas the former is acceptable in everyday life. Verhoog argues that the 'objectification' of science has led to a separation between science and ethics. It is a stimulating chapter; similar arguments are presented elsewhere in the book.

Both chapters in the final section focus on wildlife. David Cooper debates the use of a 'wildlife ethic', with his argument focusing on the possible explanations for current human sentimentality towards wildlife. Charles Bergman's chapter instils a sense of outrage at the increasing endangerment of wildlife species and the sometimes futile strategies used to save, protect or conserve them. The argument evolves into a debate about science philosophy and focuses on Descartes' view of the need to gain knowledge in order to gain dominion over nature.

Together with reviewing areas of research associated with human attitudes towards animals, animal welfare and related issues such as animal consciousness, several authors have challenged the approach to scientific methodology, especially in how we should assess animal suffering and animal consciousness. Overall, this book presents an informative and interesting read and I would recommend it to anyone involved in using animals, either for educational or research purposes.

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