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## Book Reviews

Host-Parasite Evolution: General Principles and

Avian Models. By D. H. CLAYTON & J. MOORE. Oxford: Oxford University Press (1997). Pp. 486. Price £60.00 hardback, £25.00 paperback.

The study of host-parasite interactions is a booming discipline in ecology, evolution and behaviour. More books than ever before have appeared over the past few years, and research groups continue to pop up at universities all over the world. Why this interest, and why yet another new book? Since Price's (1981) revolutionary and now classical textbook, parasites have been considered, in most of today's hot spot areas of behaviour and evolutionary ecology, as one of the most important of selective agents. Sometimes it seems hard not to believe that the whole living world is driven and explainable by the effects of parasites: natural and sexual selection; morphology; evolution of life cycles and life histories; evolution of virulence; population dynamics and demography; or even the evolution of the fundamental process of sexual reproduction with a wasteful investment in males, to name just a few. Even conservation biology appears in a new light by some recent insights, although counterintuitive, that the conservation of parasites may be important for the conservation of whole ecosystems. An end to all this development is not in sight.

Clayton and Moore's book on host-parasite evolution covers, in 17 chapters, five main topics of recent research on host-parasite relationships: the evolution of host traits and life histories through parasite-mediated natural and sexual selection; behavioural and immunological parasite defence; the effect of parasites on population dynamics and demography; community ecology of hosts and parasites; and host-parasite co-speciation. Chapters 1–12 form part I and are intended to illustrate general principles of host-parasite evolution, while chapters 13–17 fall in part II, termed Avian models, which is basically a review of all major groups of

bird parasites from viruses to brood parasites. Finally, a large appendix provides good advice for the collection, identification and quantification of various bird parasites.

Goater & Holmes (chapter 1) first analyse the foundations of some basic assumptions required for parasite-mediated natural selection, namely the correlation between parasite numbers and host fitness, and the covariation between parasite numbers and selected traits. The focus of their second analysis, the heritability of resistance traits, seems too narrow given their much broader aim to show that parasite-mediated natural selection is of relevance. The third part of the chapter analyses constraints acting on the evolution of parasite resistance and tolerance. The following chapter by Wakelin & Apanius is a highlight for those interested in the evolution and genetic control of immune defence. Embedded in a wealth of information is the central message that the degree to which hosts can control the level of parasitic infection through immune responses is genetically determined. Concerning the biological step preceding host defence by immune responses, Hart (chapter 3) provides a literature review on the evidence for behavioural control of parasites. Hillgarth & Wingfield (chapter 5) present, at an endocrine level, the many facets of parasite-mediated sexual selection, and provide an excellent state-of-the-art review of the experimental evidence regarding the effects of steroid levels on parasite intensity, of parasites on steroid levels, and of sexual hormones on the expression of secondary sexual characters. The evidence that circulating levels of testosterone are immunosuppressive or increase the level of parasite infections is actually weak, and Hillgarth & Wingfield suggest that corticosterone rather than testosterone acts as the regulatory hormone for the interaction between parasites and secondary sexual characters as proposed in the immunocompetence handicap hypothesis. Moller (chapter 6) reviews the interaction between parasitism and life-history evolution. One of the basic elements

of life-history theory is reproductive effort, and Moller takes it as an example to illustrate both how parasites affect host reproductive effort and how reproductive effort affects parasitism. He also provides the link between the immunocompetence handicap hypothesis and the evolution of life histories that I had missed in the previous chapter. Hudson & Dobson (chapter 7), using [Anderson & May's \(1978\)](#) seminal theoretical analysis, discuss the conditions required for parasites to regulate host populations. The distinction between micro- and macroparasites is interesting, although I missed, for a review chapter, more thorough reference to the literature. Dobson & McCallum (chapter 8) apply the current knowledge of host-parasite interactions to bird conservation. The risk of introduction of pathogens in wild populations arising from captive breeding and release of endangered species is illustrated and the preventive measures required are discussed. Finally, recent parasite community models ([Dobson & Roberts 1994](#)) are taken to show that parasite diversity will decrease with high host fecundity and reduced longevity, with dissimilar parasite life histories, with low parasite aggregation, and with increased host density. [Simberloff & Moore \(chapter 9\)](#) point out that our understanding of the community ecology of parasites is hampered by a poor knowledge of intra-communities and the autoecology of parasites. Factors governing species richness, and parasite assembly rules for predicting coexistence of parasite species in host individuals, populations and ecosystems are discussed. Gregory (chapter 10) analyses the value of the various comparative methods used for understanding the evolution of parasite communities, and concludes that experimentation and manipulation of parasite communities will be a more efficient research strategy than even more surveys and comparative analyses. Both of the last two chapters of part I of this book review the methods for analysing host-parasite co-speciation. While Hoberg

et al. (chapter 11) emphasize the use of Brook's parsimony analysis for the demonstration of co-speciation, Paterson & Gray (chapter 12) believe that component analysis is more powerful and allows more detailed inferences about the coevolutionary history of hosts and parasites.

I was surprised that in several of the chapters literature citations stop in 1994, which seems way back for a book appearing in 1997 and in a field with an exponential rate of productivity just in the past 3 years. Nevertheless, most chapters indicate ideas and priorities for research still not undertaken today. In contrast to some other recent books on host-parasite evolution containing rather original research articles, all contributions to this edited volume are reviews, and as such most of the chapters provide a good starting point to the specific themes and an access to the recent original literature. It is useful for students who intend to work on one of the topics outlined above, or for teachers of an advanced course on host-parasite evolution, and certainly a worthwhile acquisition for biological libraries. The beautiful cover illustration, depicting a colony of tick-infested macaroni penguins, will imprint the reader's memory with what is clumsily called 'aggregated parasite distribution' or 'overdispersion'.

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