

## BOOK REVIEW

### A review of *Evolutionary Ecology of Parasites*, by Robert Poulin

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**Evolutionary Ecology of Parasites.** 2nd Ed. Robert Poulin. Princeton University Press, Princeton. x+332pp. Softcover \$39.50. ISBN10: 0-691-12085-4. ISBN13: 978-0-691-12085-0.

Several books that address the ecology and evolution of parasites have recently appeared (e.g., Combes et al. 2001; Frank 2002; Hudson et al. 2002; Thomas et al. 2005; Collinge and Ray 2006; Poulin 2007). They are an indication of an active field and that more ecologists and evolutionary biologists are discovering parasites as great study systems. At the same time parasitologists are increasingly realizing that ecology and evolution shape their study subjects and are thus worth considering. So, a second extended edition of *Evolutionary Ecology of Parasites* is certainly timely.

The book starts with an introductory chapter clearly stating the scope of the book as evolutionary ecology of protozoan and metazoan parasites (not of the host–parasite interactions) of animals. It also contains a table that is typical of many sections of the book in that it presents “some of the major taxa of metazoan parasites of animals” and leaves the reader wondering what exists beyond this selection and why we only need to know about this subset. The remainder of the book can be divided into three sections: Poulin first discusses how the life-history traits of parasites have been and are being shaped (Chapters 2–5), and then moves up to the population (Chapters 6 and 7) and community level (Chapters 8–10).

The section on parasite life history contains both the weakest (Chapter 3) and one of the best chapters (Chapter 5), in my opinion. Chapter 3 basically says that there are no general patterns in host specificity. If true, this is interesting but most parts of this chapter are quite speculative and lack testable hypotheses. A quarter of the space used would suffice to get this message across. Chapter 5 deals with host exploi-

tation strategies and gives a good introduction to virulence evolution.

The section on population level aspects (Chapters 6 and 7) discusses the patterns of parasite aggregation in their hosts, what might cause the observed aggregation and how it links to parasite population dynamics, central themes in parasite ecology and epidemiology. A key message of these chapters is that most host individuals harbor such low parasite densities, that many processes which are often invoked (e.g., density-dependent regulation of parasite population sizes) will usually be irrelevant. The chapters are a stimulating read but they suffer from a weakness that is apparent throughout the book: the general introductions to the underlying theories could be done much better (even in a very concise format, as e.g., in Hudson et al. 2002), which would increase the appeal of the book to nonspecialists and make it more useful for courses.

The last section starts with a discussion of resource competition between parasite species. Other types of competition—let alone facilitation—are not discussed. The second part of Chapter 8 is interesting because it gives convincing examples of how competition can lead to shifts in fundamental and/or realized niches of different species. Chapter 9 discusses factors that lead to the observed parasite communities in single host individuals and will be useful if you want to model transmission dynamics with multiple parasite species. Owing to his strict focus on the parasite, Poulin often treats the host as a black box. In this chapter, the limitations of this approach become especially apparent because clearly the host influences its parasite community in many important ways, which is only superficially discussed. Chapter 10 shows that parasite richness clearly correlates with host population density but, somewhat counter to common thinking, not with host body size, geographical range and host lifespan. Hopefully, in a future edition we will also read a discussion why this (or most other patterns described) might be so.

The last chapter is called “Conclusion.” I was expecting to find a few pages of conclusions pulling everything together and giving a concise research agenda. Instead, Poulin merely concludes the book (conclusion, not conclusions—the “s” matters). He gives two examples of processes from applied areas (environmental change and parasite control) that could drastically influence parasite evolution and that should warrant more attention by politicians and funding agencies. He ends by giving his vision of the future direction of the field: a marriage of more experiments and more (well done, phylogenetically corrected) comparative studies both addressing the same questions.

Sometimes books are written that are not really needed because there are enough other good books on the topic. This book is clearly not one of them because few good books on the subject exist, but there is still plenty of room for another book on the same topic because this one is very narrowly focused.

I discussed this book with a group of students and researchers comprising various biological or parasitological backgrounds. The parasite evolutionary ecologists among us had mixed feelings about the book but those coming from medical parasitology or without much prior exposure to parasitology were stimulated to take a new perspective on old questions. The medical parasitologists were also surprised about the wealth of knowledge on parasite ecology available. This alone justifies the book. Poulin certainly covers helminth evolutionary ecology very well and does a good job arguing that evolutionary ecology and parasitology need to be brought together to the benefit of both. However, my general impression was not one of a razor-sharp review of an emerging field based on a rigorous theoretical foundation. I more had the impression of a longish account by a very knowledgeable field ecologist who tries to arrange much of the existing literature in the right sequence to make an evolutionary story of it.

The main problem I had with the book was that it is much too narrow. Frustratingly so! This book is about helminths (and to a lesser degree fish ectoparasites), not parasite evolutionary ecology in general. The occasional other examples that slip in (almost by accident, it seems) do not change that. I am all for focused books. But neither the title nor the text on the back cover reflect this taxonomic restriction. Nor is there any conceptual justification for it, which I found all the more annoying because Poulin repeatedly emphasizes that this book is about concepts and big theories. Maybe the author should think about his own words more carefully for future editions: “Of course, we will need to establish further model species in all major taxa to achieve higher levels of generality; after all, it would not be prudent to base all our conclusions on a handful of parasite species that do not capture the full spectrum of nature’s possibilities” (p. 268). I couldn’t agree more. But the main problem here is not that it is not being

done but that Poulin chooses to ignore it. It is astonishing how completely he ignores the huge field of medical parasitology despite the wealth of knowledge that the field has generated. Probably that is because medical parasitology is strongly concerned with the host and he makes a point of focusing only on the parasite (which is ok, but doesn’t make the book more interesting). But given the much greater resources and manpower in medical research, it has generated plenty of results that would be suitable even for a book as narrowly focused as this one.

The comparative approach is a central theme of the book, which I found a bit odd because a main lesson I learnt from this book was that this approach—if performed properly—in most cases fails because not enough independent data points can be gathered to say anything meaningful. Furthermore, many of the hot topics in parasite evolutionary ecology, e.g., the evolution of virulence and resistance, involve fast evolving traits that are unlikely to leave any phylogenetic signal and can thus not be addressed by the comparative approach. A stronger emphasis on such topics would do the field more justice. For instance, the rapid evolutionary responses of parasites to disease control measures touched on in the concluding chapter are much better investigated than the brief mention makes believe. They are of fundamental interest, not just as “strong arguments to lobby funding bodies and decision makers to grant a place for parasite evolutionary ecology near the top of the list of priorities” (p. 263).

I found the book too long for the content. It would gain if 50% were cut out (which seems possible without losing too much information) and replaced with content from other systems, or if it were shortened and given a more precise title. The table of contents is virtually unchanged from the first edition but the second edition weighs about three times as much, which appears to be mainly due to the addition of a large number of new studies. Readers who liked the first edition but were missing some meat on the bone will be delighted about that. On the other hand, I sometimes found myself drowned in too many examples. Less would have been more in some cases.

Finally, from a frontrunner of the field I would have liked to hear more concrete and stimulating open research questions, not just “more research is needed” or the call for “a marriage between experimental studies and comparative studies” (p. 269).

I can fully recommend the book to anyone who wants to or does not mind reading an evolutionary ecology book primarily on helminths. People who want a comprehensive overview or a general introduction of the field of parasite evolutionary ecology may be disappointed. As an evolutionary ecologist working with nonhelminthic parasites, I may not have read it had I been aware of the narrow taxonomic focus. I got too little out of too many pages and I suspect that

researchers reading this journal will have issues with Poulin's approach to discuss patterns but not possible mechanisms generating them.

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