

then chooses the one that gives the 'truth'. In this the way, one could claim to be making an objective statement when asserting that 'some methods of phylogenetic analysis give the wrong answer'. This used to be called *a priori* character weighting, and was considered evidence that systematics could never be an objective science; now, in an Orwellian twist, it is considered by some to be the only proper approach. Using this traditionalist approach, one can provide explanations about virtually any area of evolutionary diversification without *a priori* reference to any phylogenies, then using that information to determine which phylogenetic reconstruction is correct (e.g. contributions by Hollocher, Schluter and Losos in the Grant volume).

The realist perspective claims that phylogeny leaves traces that can be discovered objectively by sampling the real world. Disagreement between samples from the real world and a particular model is taken as objective evidence that the model is flawed. For realists, the conventionalist approach introduces a degree of circularity that buffers hypotheses from potential falsification. For conventionalists, there is something suspicious, not to say threatening, about a method that could overthrow conclusions based on more than 20 years of work. Powell, for example, makes extensive use of phylogenies in his chapters on genome evolution, molecular evolution and development – all relatively recent areas of research – but none in his ecology and speciation chapters, based on research reaching back more than a generation.

Neither conventionalists nor realists generate truth. Popper preferred the realist approach because it permitted easiest refutation of hypotheses. But most of the time scientists do not worry about refuting hypotheses – they use hypotheses to focus their research. Popper thus concluded that conventionalists and realists coexist in relative harmony except during times of conceptual upheaval. Tensions within evolutionary biology at the moment could thus be cause for celebration. By the same token, it is during such times that we need strong statements from traditionalist camps. Otherwise we risk losing our way, at best reinventing the wheel, at worst wasting our time and losing knowledge in the process. These books are excellent at emphasizing the successes of their approaches, and also at presenting a detailed list of questions to be answered. Their authors defend traditionalist, and generally conventionalist, views on topics significant to almost every area of evolutionary biology, helping establish a historically constrained arena within which progress towards the next phase in the evolution of evolutionary theory can take place.

Daniel R. Brooks

Dept of Zoology, University of Toronto,
Toronto, Ontario, Canada M5S 3G5
(dbrooks@zoo.utoronto.ca)

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Ultimate parasites

Evolutionary Ecology of Parasites. From Individuals to Communities

by *Robert Poulin*

Chapman & Hall, 1998.
\$55.00 hbk (x + 212 pages)
ISBN 0 412 80560 X

Consider the following statements, which, to a reasonable approximation, are true. Most organisms are parasites. Their natural habitats can be easily replicated under controlled conditions in the laboratory. Parasite evolution occurs on timescales shorter than that of a grant or PhD. Substantially more research money is directed at infectious diseases than at organismal biology. Evolutionary ecologists are largely uninterested in parasites.

Why is this last statement correct? Here's my guess: most evolutionary ecologists are attracted to organismal biology because they enjoy muddy-boots natural history. Parasite natural history is mostly not like that. Animal models (and associated blood and guts) are simultaneously the essence of parasitology and an anathema to those who want to watch birds. David Attenborough may also be to blame: he has yet to televisualize successfully the substantially more diverse, though perhaps less technical, life histories of parasites. For myself, extensive therapy provided by stimulating colleagues was required to overcome a strong aversion to parasites acquired during the dry taxonomic tour that constituted my undergraduate parasitology experience.

Whatever the reason, a consequence is that we know relatively little about the evolutionary ecology of parasites, as this book makes clear. By ignoring hosts, an area of host-parasite interactions that has received attention from evolutionary ecologists, Poulin is left largely with questions.

As he points out in his conclusion, a pervasive theme of all chapters is the need for further work. This is both the strength and weakness of the book. There is a strong feeling that the book is premature, but the stark shopping list of ignorance is provocative – almost a call to arms. I imagine Poulin will feel well pleased if, as a consequence of publishing now, future editions are able to be fuller and more satisfactory.

I hope they are. Parasites pose some very interesting challenges. The purely ecological ones of population dynamics, community structure and the like, which are well introduced by Poulin, have attracted considerable interest. However, the challenges for evolutionary ecologists have received substantially less attention but are at least as great. For example, many parasites have highly improbable life cycles. If finding the definitive host is unlikely, why incorporate another host into the life cycle? And why make that second (or third, or fourth) host an obligate requirement? For example, many mammals become infected with nematodes when eating contaminated herbage. Some of those nematodes will die unless they have been through an intermediate host; others in related taxa have no such requirement. Similarly, why are some parasites so host-specific, whereas others are generalists? What is responsible for the huge diversity in life histories? Cross-species variation in worm fecundity, for example, makes avian clutches look invariant. Why are some parasites more damaging to their hosts than others? Some hypotheses supposedly address some of these questions. The empirical support for these, which Poulin does a good job of summarizing, is frequently flimsy or indirect.

The book is aimed at advanced undergraduate or graduate courses in parasitology. (Students in evolutionary ecology might find the descriptions of theory frustratingly superficial and that they need to have a conventional parasitology textbook on hand for the biological details.) In this, it is a direct competitor with two other texts^{1,2}, which also cover topics such as hosts, parasite genetics and biogeography. The idea of taking evolutionary ecology into parasitology is laudable, and Poulin introduces relevant theory well enough for such an audience. However, I cringe at the thought of a budding parasitologist comparing the sophisticated (albeit rather theory-free) understanding of the proximate mechanisms described in, say, a parasite immunology course, with the theory-laden, rather data-free ultimate explanations offered in this book. This is not Poulin's fault – it is the state of the play. It would be nice to think that the course Poulin envisages might help balance theory and data in both mechanistic and evolutionary studies of parasites, but I can't help worry that we are so far

behind with data (and in the glamour stakes) that parasitology graduates will stick with their conventional research areas. Progress is surely more likely to come from evolutionary ecologists looking for intellectually exciting (and fundable!) openings.

What are the hopes for progress? Poulin expects rapid advances. I am more pessimistic, though I would be delighted to be proved wrong. Field observations on parasites are usually difficult and their scope limited. Experimental work usually requires at least two very different organisms be maintained. Fitness assays are often indirect, involving organisms that are out of sight. Many traits of interest, such as life cycle complexity and host specificity, usually do not vary within a species. Quite why that should be so is an interesting question in its own right, but that fact rules out intraspecific comparisons. Poulin argues that cross-species studies will be of particular value once the absence of good phylogenies is overcome. That problem is rapidly resolving itself (e.g. Ref. 3), but a more worrying problem, and one less easily rectified, is that degrees of freedom for comparative work are often in short supply. Major transitions in life cycle complexity, for example, are often widely dispersed phylogenetically and are associated with huge radiations. Evidence from impressively large cross-species data sets can rapidly collapse into little more than anecdote when modern comparative methods are brought to bear.

Despite these technical difficulties, an evolutionary ecology of parasites is worth the effort. It would be intellectually satisfying (and a great deal more interesting to students) if the facts which form parasitology could be made sense of functionally rather than taxonomically (e.g. Refs 4,5), an approach that is now second-nature when presenting the facts of animal behaviour⁶. Moreover, such a framework could open the way to prediction. What will be the outcome of the selection imposed by medical and veterinary intervention? What sort of immune response should be functionally important in particular circumstances? Is this parasite likely to be host-specific? When is it likely to jump into new host populations? There are also questions of general interest, which seem more readily tractable in the parasite context. For example, a satisfactory explanation of the variation in host specificity might shed light on the specialist versus generalist debate. Similarly, focusing on the issues of group selection, rather than the associated emotion, is relatively easy in the context of within- and between-host selection. But even more generally, evolutionary ecology is about explaining diversity. Most organisms are parasites (all hosts have at least one host-specific

parasite); if the Creator really did have an inordinate fondness for beetles, He must have had an inordinately inordinate fondness for beetle parasites. To ignore the evolutionary ecology of parasites is to ignore the majority of life.

Andrew F. Read

Institute of Cell, Animal and Population Biology,
University of Edinburgh, Edinburgh, UK EH9 3JT
(aread@holyrood.ed.ac.uk)

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Bird biodiversity

Endemic Bird Areas of the World. Priorities for Biodiversity Conservation

by A.J. Stattersfield, M.J. Crosby, A.J. Long and D.C. Wege

Birdlife International, 1997.
£37.00 pbk (860 pages)
ISBN 0946 888 33 7

CDROM: Birds of the World – A Multimedia Encyclopedia

Ransom, 1997.
£14.99
ISBN 1 863 89 1748

Endemic Bird Areas of the World looks at the biodiversity of birds on a global scale. In brief, roughly 25% of the world's 10 000 bird species have restricted ranges. If all the ranges of all these 2561 species are drawn on the same map, not only do many of them overlap, but most are concentrated in the same areas. Indeed, 93% of these species are encompassed by 218 areas which together make up only 1% of the land surface of the world. These areas are called Endemic Bird Areas – EBAs. Some 77% of the EBAs occur in the tropics, and the countries containing the largest numbers of them are Indonesia, Mexico, Brazil, Peru,

Colombia, Papua New Guinea and China. EBAs vary from only a few square kilometres to >100 000 km² and the commonest habitats are forests, especially lowland tropical forest and montane moist forest.

The EBAs are drawn up on the basis of restricted-range species. These are species of landbird which are thought to have had a breeding range of <50 000 km² throughout recorded historical times (= since 1800). A few species which were historically widespread and now have ranges smaller than this are omitted. An EBA is then defined as an area which encompasses overlapping breeding ranges of restricted-range species such that two or more restricted range species are entirely included within the boundary of the EBA.

It would only be possible to produce a book like this for a very few, if any, groups of animals or plants other than birds. However, from what is known it is clear that these EBAs encompass habitats which are very important for the preservation of many other endangered taxa; thus, birds serve as a marker for areas with generally high biodiversity. For example, there is an overlap of more than 60% with similar endemic areas drawn up for plants. But this is not always true; for example, plotting the ranges of species with restricted ranges in the UK does not always show close matches between different taxa, but of course the very depauperate fauna of disturbed areas such as the UK may not be typical of richer, less disturbed tropical areas. Also, there are strong reasons for believing that the EBAs will turn out to be key areas for many taxa.

Importantly, the endangered species occupying these EBAs once had much less restricted ranges, since these EBAs once covered at least 2% of the earth's land surface but now take up only 1%. In other words, they have already been reduced by 50% on average and in some cases – obviously – much more.

The first 50 pages or so of the book provide the methodology and some analyses of the data collected, together with lists and maps. There follows a 40-page review of the regions, again with clear tables and maps of the EBAs. The 'guts' of the book are the 550 pages where each of the 218 EBAs is considered separately. An impressive amount of data is packed into the two pages or so that are given to each area. The information is inevitably compacted, but there are a clear introductory interpretation and clear keys to the abbreviations.

There follows a list of 138 'secondary areas', defined as 'an area which supports one or more restricted-range bird species, but which does not qualify as an EBA because fewer than two species are entirely confined to it'. A 45-page appendix which lists restricted-range bird species by family