

Evolutionary Behavioral Ecology

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encompassing title and lofty goal of integrating the broader issues of biodiversity loss and climate change.

After the book defines wildlife as “vertebrate animals,” and toxicology as “effects of toxic chemicals,” some chapters stray far from this focus. The article on munition-related compounds focuses on daphnia and soil invertebrates, and states that there has been little work done on birds and mammals—both major examples of “wildlife.” The chapter on pesticides and biofuels is about neither their toxic effects nor about wildlife. The chapter on contaminants and disease, one I looked forward to reading, is primarily an overview of infectious diseases of wild and domesticated animals, with a bit about activity and behavior of animals. Only a few pages are devoted to how contaminants can alter susceptibility to disease, which presumably should have been the major focus of a chapter in this particular book. I also looked forward to reading a chapter on climate change effects on wildlife toxicology (temperature increase and ocean acidification are likely to increase the toxicity of most chemicals); I was surprised, however, to find a chapter that might have been titled instead “Climate Change 101”—a general introduction to the issue that did not address wildlife toxicology at all. Although the chapter is a good overview of the topic, I find it hard to imagine that environmental professionals, the book’s intended audience, would gain much from it. To try to cover causes of climate change and its effects in the marine and terrestrial environment is a task for multiple volumes of review articles. Lastly, the topic of most relevance in this book—the effects of climate change on wildlife toxicology—isn’t covered at all.

Perhaps this book should have been given a different title. But even if it were, it would be hard to see the “glue” that holds this collection of papers together. In the final chapter, Kendall looks forward to a future with greater integration. And with that I can only agree.

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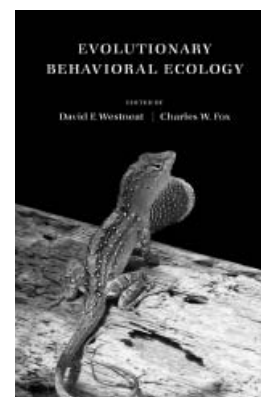
BEHAVIORAL ECOLOGY—ONLY IN THE LIGHT OF EVOLUTION DOES IT MAKE SENSE

Evolutionary Behavioral Ecology. David F. Westneat and Charles W. Fox, eds. Oxford University Press, 2010. 664 pp., illus. \$49.95 (ISBN 9780195331929 paper).

Several recent volumes address specific topics in behavioral ecology, such as foraging theory and sexual selection, but a recent synthesis comprehensively assessing the current state of research in all areas of behavioral ecology has not been presented since the 1997 updated edition of Krebs and Davies’s *Behavioural Ecology: An Evolutionary Approach*. As the titles of that volume and this one suggest, behavioral ecology is best understood in context of the fundamental concept uniting all of biology: Darwin’s theory of evolution. In *Evolutionary Behavioral Ecology*, editors David F. Westneat and Charles W. Fox have compiled an immense collection, drawing upon the expertise of more than five-dozen researchers in the field. The editors charged these authors with the task of making the volume “accessible to students,” particularly first- or second-year graduate students, and most chapters are understandable to readers at this level, depending on their prior experience. I found the approach straightforward and easy to follow in subdisciplines with which I was strongly (foraging theory) or moderately (sexual selection) familiar, but I had more difficulty with chapters on quantitative genetics and genomics.

A few chapters cover familiar ground in behavioral ecology (e.g., foraging

theory, predation risk, group behaviors, and sexual selection); however, each chapter’s authors give comprehensive summaries of keystone literature (e.g., R. L. Trivers’s seminal work on parent-offspring conflict) and bring the reader up to date, with an emphasis on findings published in the past decade. The examples are generally well chosen to unite predictions made by older literature and include tests of those predictions using both theoretical and well-constructed empirical approaches. Although such examples are illustrative and speak to the mountain of evidence for how natural selection can act on behavior, they are numerous to the point of being overly exhaustive at times. This reflects the thorough surveys done by



the authors, but it can cause the reader to become bogged down in case studies at the expense of an understanding of general concepts.

One cannot fault the conceptual discussion of the evolution of eusociality for being too thorough, however. Despite E. O. Wilson and colleagues’ recent criticism of kin selection theory and the concept of inclusive fitness, chapters 18 (Gardner and colleagues) and 19 (Queller and Strassman) carefully describe the conditions that favor altruism, cooperation, and the evolution of animal societies. Critics of kin selection theory and its ability to predict social behavior in animals would do well to examine empirical examples of long-tailed tits and slime molds

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provided in chapter 18. Furthermore, detailed derivations of Hamilton's rule and a partial differential equation approach to kin selection models—both accounting for the interaction of multiple individuals with different phenotypes—should dispel the notion that kin selection theory is no longer useful. Of course, neither kin selection nor the asymmetric relatedness of haplodiploid species necessarily results in the evolution of eusociality. Queller and Strassman acknowledge that cooperation is not explained by relatedness alone, and describe the implications of multiple mating by queens in haplodiploid hymenopterans, for example. Gardner and colleagues also mention the application of these principles to the evolution of cooperation in human societies, though I was disappointed to see that this subject was not considered in more detail in one of the “Extensions” chapters. Such a discussion would have been timely and concurrent with several recent papers in the peer-reviewed literature on the evolution of morality.

For the theory-minded reader or student, the chapters of this book vary in accessibility and extent of theory-related detail. In chapters with the ideal layout, the main text focuses on the generalities, whereas the details of theoretical models are presented in several boxes inserted within the chapter. For example, Earley and Dugatkin (chapter 17) explain the selective advantages of group behavior, and Nonacs shows (in box 17.2) the derivation of models that predict why reproductive success in groups is unequal—and points out several limitations of the approach. In other chapters, however, the boxed text provides yet another example that could have been incorporated into the text or omitted completely (e.g., a study supporting a general principle). Some chapters are strongly analytical and may be completely accessible only to specialists, such as the one by Wolf and Moore (chapter 14) that modifies quantitative genetic models to predict the amount of heritable variation of a trait due to the “environmental” effect caused by social interactions with

other individuals (also a genetically variable set of influences). Perhaps the most effective discussion of quantitative approaches to making testable predictions for behavioral studies is Ydenberg's “Decision Theory” (chapter 8). The chapter is an excellent transition from the “Foundations” section of the book (see below) into the more contemporary approaches to behavioral ecology discussed later.

Experts in genomics may wish for more than the chapter toward the end of the volume (chapter 28) by Grozinger, but the nonspecialist is introduced to modern molecular techniques such as high-throughput assays to help search genomes for specific traits and genes under selection. The identification of a trait under selection is particularly challenging in behavioral ecology because the behavior as a phenotypic expression may be a combination of several traits that combine in response to environmental cues in different ways. Thus, it is not always clear what the target of selection may be. Nevertheless, examples of the identification of behaviorally related genes are scattered throughout other chapters, and one can sense that the relatively low number of these examples reflects a field still under development.

Compiling a comprehensive volume on evolutionary behavioral ecology is an enormous undertaking; the result, in this case, is proportional to the task. This volume certainly exceeds the capacity of a single graduate seminar; arguably, a two-semester course could be designed using this text, assuming students already have a grasp of the basic concepts. The eight-chapter “Foundations” section, with general reviews of the concepts of adaptation, natural selection, fitness, and phylogeny, would provide enough material to fill out an upper-division undergraduate course. For specialists designing graduate seminar courses, the other major sections, into which the editors have grouped the remaining chapters, could each function as material for a single course (particularly if the suggested further readings and other

literature were incorporated). Section II (“Decision Making”) and section III (“Ecology of Behavior”) could be combined.

Behavioral ecology is a distinctly Darwinian science, and the material in *Evolutionary Behavioral Ecology* shows that behavioral traits are actually the easiest to study in terms of how natural selection acts to determine their relative fitness. Despite the challenge of linking those behavioral traits to specific genes, many of the most informative examples of natural selection as a driving evolutionary force come from this field. The contributing authors of this volume bring each area of study up to date by summarizing current literature. *Evolutionary Behavioral Ecology* should set the standard for the field for another decade or two.

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