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SURVIVAL, REPRODUCTION, AND BEHAVIOR

Krebs, J. R., and N. B. Davies. 1993. **An introduction to behavioural ecology**. Third edition. Blackwell Scientific Publications, Cambridge, Massachusetts. xii + 420 p. \$36.95, ISBN: 0-632-03546-3.

In addition to their edited volumes for specialists in behavioral ecology, Krebs and Davies have published two previous versions of this textbook aimed at introducing the field to undergraduates and others seeking to understand an evolutionary approach to the study of behavior. Although the general topics are the same as in previous editions, examples have been updated and sections on new techniques such as DNA fingerprinting added.

All of the expected topics are covered in the 15 chapters: decision-making and optimality, predator-prey relations, competition, sociality and cooperation, altruism, sexual selection, mating systems, parental care, and communication. The authors also include sections on hypothesis-testing and the comparative method, and a concluding chapter with some caveats about the validity of basic assumptions used in the study of behavioral adaptations. While clearly suitable for a course in behavioral ecology, rather than a more general animal behavior course, we believe the book may be aimed too high for the average undergraduate, especially one without a previous course in evolution. Terms such as “polymorphism,” “phylogeny,” and “stabilizing selection” are used without definition and will require some supplementary help from the instructor. The examination of some difficult concepts in boxes interspersed throughout the text helps ameliorate some of these shortcomings. The introduction to natural selection, on the other hand, is superb; juxtaposing a modern, genetics-based outline with Darwin’s original verbal syllogism should make this topic accessible even to those students who are still shaky on the subject of meiosis.

At the outset, the example-oriented approach is made clear: “. . . we prefer to illustrate the theory with examples after a very brief general introduction, rather than developing long, abstract, theoretical arguments.” This technique has both advantages and disadvantages. On the positive side, most students can better appreciate a concept such as evolutionary arms races once they are given an illustration of its operation in cuckoos and their hosts. Many students, however, will probably have difficulty generalizing from the examples given to an understanding of the topic as a whole; we could all recall instances of students defining terms by saying, for instance, “Polygyny is when a male red-winged blackbird has a lot of

females in his territory,” instead of actually synthesizing the information from the various examples. Furthermore, the opportunity arises to quibble with the authors’ choice of examples, with various members of our group faulting the paucity of examples from invertebrates, amphibians and reptiles, field studies of predation, and studies by non-British scientists.

The first two chapters lay the groundwork for the study of behavior, and explain how the comparative method can be used to answer questions about the evolution of behavior. Assuming students understand the pitfalls of nonindependence due to unknown phylogenetic relationships, the discussion is thought-provoking and complete. Oddly, however, the comparative method is then given short shrift in the rest of the book, with virtually all studies cited coming from experiments in either the field or laboratory. We also appreciated the concluding chapter, which points out that “even our basic assumptions are still very much disputed in the literature,” and felt that this critique should have been included with the earlier chapters on how scientists study behavior. Instructors might wish to assign this chapter early in the term.

The chapter on decision-making promotes optimality theory a bit too vigorously as the solution to environmental variation in resource availability, although the flexibility and power of this approach are persuasively displayed. The fundamentals of evolutionary arms races and of competition theory are clearly demonstrated in the following chapters, through detailed examples illustrated with excellent photographs and drawings, with pertinent data given in useful tables and figures. All figures are redrawn specifically for the book, which helps make the use of data from individual studies more understandable and is a nice touch sometimes overlooked in textbooks.

An agenda is again apparent in the chapter on fighting and assessment, which promotes game theory to the exclusion of other approaches. Here, as elsewhere in the book, some historical background might have been useful to help students understand how conflict has been viewed by biologists, with a recent move away from the Lorenzian “good of the species” view of the use of convention in displays. Indeed, the field of behavioral ecology is mainly presented as a *fait accompli*, with the exception of a nod towards Tinbergen, rather than a field with roots reaching back into comparative psychology, ethology, and genetics.

Sexual selection, sex ratio theory, and mating systems are all covered thoroughly and with impressively up-to-date ref-

erences. We noted with distress, however, the lingering male-oriented viewpoint and associated sexist vocabulary; the terms "ardent males" and "reluctant females" are, if anything, worse than the traditional adjectives of "competitive" and "coy." Females may be discriminating, but this says nothing about whether they are passionate. Mating systems are discussed twice, first in circumstances without parental care and then with it; in addition to being confusing, this division leads to polygyny being discussed twice and monogamy and polyandry once. Polyandry has often received an uncomfortable treatment in the literature, and this was no exception. The Tasmanian native hen, a species in which a female is mated to two males simultaneously, is said to exhibit "wife-sharing," when similar cases of single males with multiple females are never called "husband-sharing." This terminology is inappropriate. Recent examinations of the role of multiple mating by females of many species could have been more thoroughly considered. The chapter on alternative breeding strategies is clear and well-illustrated, concluding with a concise and interesting discussion of sex change in fishes, although a section titled "Sex change versus sneaking" is actually an explanation of the lack of sequential hermaphroditism in mammals, and should have a more appropriate title.

The chapter on selfishness and altruism begins with the best explanation of kin selection and the calculation of coefficients of relatedness we have seen. Kin recognition, mutualism, reciprocity, and the Prisoner's Dilemma also receive stimulating treatments, perhaps because the theory is explained more thoroughly than in other chapters with less reliance on examples. Short discussions of mutualism and manipulation

point out that what may appear to be altruism at first sight may be selfishness if cooperation can enhance individual survival (as in mutualism) or if recipients are manipulating the donor.

Chapters on cooperation and helping in birds and mammals (the authors claim to discuss fish as well, but include only one brief example) and on altruism on the social insects are likewise thought-provoking and rich with examples. The comparison of cooperation in the two groups of taxa is excellent, and should allow students to synthesize information about these two often needlessly separated behaviors. The chapter on signalling behavior is a good mix of classical ethology and behavioral ecology, and makes the point that understanding of the mechanisms behind behavior can give insights into the evolutionary forces which molded the signal's design.

The book is well-written and beautifully produced, with remarkably few typographical errors. The addition of color photographs, new to this edition, enhanced the text. For courses in behavioral ecology at institutions where students can receive sufficient supplementary or background information about evolution, the volume has no competitors.

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