

Preface

An understanding of the natural world and what's in it is a source of not only a great curiosity but great fulfillment.

—Sir David Attenborough, September 2004, during a break from filming bolas spiders at the University of Kentucky's Spindletop Farm

The diversity of ways in which organisms interact with their environment, including members of their own species, other species, and the abiotic world, is astounding. The field of behavioral ecology explores the role of behavior in these interactions. Behavioral ecologists are typically interested in a functional understanding of behavior: why do animals behave the way they do, and make the decisions that they make? How are animal decisions and behaviors shaped by evolution in response to ecological and/or social conditions that they experience? Such questions have turned out to be surprisingly complicated, requiring a diversity of approaches, from mathematical modeling to biogeographic analyses to field manipulative studies, and integration among fields of study, including psychology, evolutionary biology, physiology, molecular biology, and even economics, among others. The insights gained by behavioral ecologists have generated considerable controversy over the years, spurring the field to move in new directions.

Two of the most deservedly famous individuals in behavioral ecology are John Krebs and Nick Davies. Though the study of behavioral ecology did not start with them, its definition as a field of study was in large part due to their immensely influential book, *Behavioural Ecology: An Evolutionary Approach*, published in 1978. That single book pulled together the variety of behaviors and ideas that had been the focus of researchers interested in functional explanations. Through four editions,

the latest in 1997, the Krebs and Davies volumes brought both conceptual clarity and empirical excitement to the field. Probably every practicing behavioral ecologist has gained insights from these volumes. Although these editions still make for compelling reading and provide excellent overviews of the logic and methods of the field, they no longer reflect the full scope of the field: some of the material is dated, and each edition intentionally included an eclectic set of topics not broad enough in scope to form the foundation for a comprehensive, semester-long graduate class.

In *Evolutionary Behavioral Ecology* we have attempted to present the core concepts and recent elaborations upon them that define the field today—a daunting task because the field has grown substantially since Krebs and Davies' first publication. Their volumes developed in detail select topics that highlighted major conceptual developments in the field, introducing these to new behavioral ecologists and energizing the veterans. However, the field is too rich and deep to simultaneously introduce beginning students to the diversity of ideas that make up modern behavioral ecology, and present each of those fields with the thoroughness of a Krebs and Davies chapter. To accomplish our goal of making a volume accessible to students, we asked authors to focus on core concepts, presented rigorously, and not write encyclopedic reviews. We wanted authors to target their chapters directly at first- or second-year graduate students and lead them through the

main ideas that have shaped the field over the past 40 (or more) years, highlighting some of the major controversies that excite us today. Our authors were thus challenged to sacrifice detail and instead focus on major ideas that have driven the field forward. We hope students find these brief introductions stimulating and that they pursue additional readings, such as those listed in "Suggestions for Further Reading" sections, to explore ideas in more detail. Most important, we hope that readers of this book—students of behavioral ecology—will take away a sense of the vitality of a field full of brilliant insights but also brimming with unanswered questions that students themselves can contribute to answering.

Unlike many books targeted to students and the classroom, we chose to edit a collection of chapters written by others rather than to write a book ourselves. A multiauthored book has strengths and weaknesses. One strength is that these chapters are written by experts in their respective areas, and so each represents a mature perspective on the important topics. A potential weakness of multiauthored books is an inconsistency of style, level of material, and breadth of focus among chapters. We encouraged authors to follow a similar outline for chapters, and we aggressively edited those chapters to provide some consistency and to highlight connections among chapters, but variation in style and level of presentation still exists. Some of these differences, such as how much mathematical modeling is included, we think are a strength of an edited volume because this diversity reflects real variation within the field, both among subjects and among researchers within subjects: some researchers do quite well without using mathematical modeling and others depend on it, yet everyone gains understanding from it. Chapters will not all be equally accessible to the intended audience, and some authors have perspectives on their topic that differ from even the majority of their colleagues (though we've strived for balanced perspectives as much as possible). Nevertheless, we think both of these problems are potentially benefits. Students grow as professionals by being confronted with topics in which there is confusion and disagreement among professionals. Often such areas of disarray are fertile ground from which new careers can sprout.

Behavioral ecology arose from scientists mixing questions and approaches among disciplines, and to understand the state of the field today it is instructive to students to learn a bit about the historical

themes as well as the personalities involved in its development. We thus start with a chapter on the history of behavioral ecology, writ large (chapter 1), before delving into more specific subjects. The rest of sections I and II provide students with an introduction to the tools and broad conceptual ideas that underpin the entire field, regardless of specific subject. Together, the two sections are deliberately linked, albeit implicitly and somewhat loosely, to Tinbergen's (1963) four questions: mechanism (chapters 9 and 10), development (chapters 5 and 6), evolution (chapter 7), and function (chapters 2 and 8).

In sections III, IV, and V we march through the traditional topics in behavioral ecology: finding food and avoiding predators (section III), social behavior (section IV), and reproductive behavior (section V). We have sequenced chapters to provide broad, overarching concepts early and elaborations on those themes later in each section. Section VI is called "Extensions," but it could also be called "Cross-Cutting" or "Emerging Frontiers." Here authors take key ideas from behavioral ecology and apply them to subjects such as speciation (chapter 27), conservation biology (chapter 29), and human behavior (chapter 31), or they present new conceptual views (e.g., chapter 30 on personality) or techniques (chapter 28 on genomics) that seem likely to provide behavioral ecologists with new ways of elaborating on functional approaches.

Of necessity, we could not cover all subfields of behavioral ecology and, for most areas, we have touched only briefly on the diversity of exciting questions being asked. Moreover, we have asked authors to be sparing in their use of citations. We did this to encourage a focus on concepts and key developments and to limit the degree to which chapters became encyclopedic reviews. We regret if some subjects and key papers thus appear to be ignored, and we apologize to those whose favorite example, case study, or specific citation was left out of the book.

There are a few unique elements of this book that reaffirm to us the value of having a new summary of our field every 10–12 years. Just as each edition of Krebs and Davies highlighted new ideas and approaches that were changing the future of behavioral ecology, the emergent picture of behavioral ecology from our book is one of increasing sophistication of both questions and techniques. By far the most compelling advances in the field have been due to the increased use of genetic tools used

to assess relatedness both within populations (e.g., kinship) and among taxa (as a basis for constructing phylogenies). These approaches have become so well ensconced in the field they are hardly mentioned explicitly, but their impact is broad. More compelling is the increased use of molecular tools, as described in chapters 5 and 28, for understanding the genetic basis of behaviors of ecological relevance, and the insights these provide regarding function and evolution of behavior. Finally, new advances in quantitative genetics have great potential to alter conceptual approaches and empirical research on a wide array of behaviors. General theory on plasticity (chapter 6) and on indirect genetic effects (chapter 14) enhances many traditional approaches to behavioral ecology and is likely to influence many future studies.

Preparing this book involved the assistance of many individuals. First and foremost, we thank the authors, who have produced stimulating chapters and have responded well to the many demands we placed on them. All chapters were reviewed both internally (by authors of other chapters) and externally; in addition to the authors who worked as reviewers, and a few anonymous reviewers, we thank the following people for their helpful comments: Sigal Balshine, Alex Basolo, Guy Beauchamp,

Anders Berglund, Andrew Bourke, Tim Caro, Will Creswell, Jonathon Crystal, Reuven Dukas, Daniel Funk, Carl Gerhardt, Greg Grether, Paul Harvey, Ken Haynes, Natalie Hempel de Ibarra, Geoff Hill, Jerry Husak, Adam Jones, Laurent Keller, Darrell Kemp, Dov Lank, Kate Lessells, Wayne Linklater, Jeffrey Lucas, Joel McGlothlin, Molly Morris, Bryan Neff, Geoff Parker, Tommaso Pizzari, Denis Reale, David Reznick, Graeme Ruxton, Mike Ryan, William Searcy, Maria Servedio, Mike Sharkey, Ulrich Steiner, William Wagner, Jonathan Wright, and Marlene Zuk. We also thank Dov Lank and his graduate class in behavioral ecology at Simon Fraser University for providing extensive feedback on many of the chapters. Several members of our labs, notably Amanda Ensminger, Damon Orsetti, Sarah Martin, Bridget Sousa, Patricia Hartman, Ian Stewart, and Dan Wetzel, read many of the chapters at several stages and provided numerous helpful comments. The Department of Entomology at the University of Kentucky provided financial support. Both our research programs have been supported by the National Science Foundation, and that support helped us to plan and carry out this project.

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