

Preface

When undertaking this project, I knew that I had my work cut out for me. Despite the fact that the format of this book is straightforward, the subject material—cooperation—is not. In fact, there were at least two ways that this book could have been written. The first would have partitioned the book primarily from a theoretical perspective. This approach would have entailed an introductory section followed by chapters on "Byproduct Mutualism and Cooperation," "Reciprocity and Cooperation," "Group Selection and Cooperation," and "Kin Selection and Cooperation." The second way of dividing up the material would have been primarily taxonomic—that is, an introduction followed by chapters like "Cooperation in Taxa A," "Cooperation in Taxa B," and so on.

In the end, after weighing the pros and cons and talking with colleagues about each, I opted for a hybrid approach that slants a bit toward the second of these formats. Following an opening chapter on the long, illustrious history of cooperative behavior, the second chapter reviews theoretical work on the evolution of cooperation, including some recent work developed by my colleague, Michael Mesterton-Gibbons, and myself. Chapters 3 to 7 proceed to examine cooperation in fish, birds, nonprimate mammals, nonhuman primates, and eusocial insects. Within each of these chapters, whenever possible, examples are placed within the theoretical framework established in Chapter 2. Chapter 8 outlines the direction in which I hope the field will move in the future.

To even attempt to place every putative example of cooperative behavior within a single theoretical framework is beyond the scope of any single book. Furthermore, I make no pretense about even attempting to cover all studies of cooperation. As such, on numerous occasions throughout this book, I refer the reader to reviews and other appropriate literature on a specific topic. Many of these topics—for example, cooperative breeding in birds—have been instrumental in the development of behavioral ecology as a legitimate subdiscipline in biology, and I certainly mean no disrespect by not devoting space to them here. In fact, the opposite is true. I think that it would be an injustice to tackle such important questions in one section of a single chapter. No doubt some people will feel that a book on the evolution of cooperation simply must cover some topics that I have not and I apologize in advance to those who feel slighted that their work has not been covered herein.

The decision regarding which studies to include and which not to include in this book was clearly somewhat subjective and, in some cases, personal. It could hardly be otherwise when dealing with such a complex idea as cooperation. I'm sure that the method I used to select which studies to highlight will differ from that of others, and I cannot always say for certain why a particular

study was included or excluded. Let me at least, however, try to give some sense of the perilous path I took in deciding such matters.

To begin with, as mentioned earlier, some topics were simply too vast to cover. When I first proposed this book to Oxford University Press, Bob May, co-editor of the new series in Ecology and Evolution, made it clear that he was not interested in a book that simply re-hashed "classic" studies in cooperation—the sorts of studies that have already worked their way into the textbooks. I have kept this statement in mind; and while I, of course, review the "classics," they are only a small fraction of the cases covered. Whether a study is well cited or not, I always try to tie it back to some theory on the evolution of cooperation. For example, if a putative case of cooperation is directly interpretable within a theoretical framework, but has received little attention in the literature to date, that in itself makes it more likely to get coverage in this book. Unfortunately, many cases of cooperation do not neatly fall into one category or another. With respect to such studies, they were chosen when I believed that, in principle, they could be deciphered—that is, experiments could be constructed to help us fit this behavior into some sort of theoretical framework—the overriding theme being that the reader be provided with as broad an overview of the evolution of cooperation as possible. Again, subjectivity and personal biases are inevitable in such a process.

Whenever possible, within each chapter, I tried to address examples of cooperation that: (1) fell into different categories of cooperation—that is, byproduct mutualism, reciprocity, group selection, kin selection, or some combination of these, (2) covered different contexts in which cooperation took place—for example, foraging, anti-predator behavior, and so on, and (3) spanned a number of different species within a particular taxon. This was not always easy, and no doubt others might have approached the task with a different set of criteria. Last, I tried to choose cases that I thought best captured the essence of cooperative behavior, or showed the potential to do so in the future. I readily admit that this was the most subjective element in my decision-making process, but it is arguably the most important as well.

With the exception of Chapter 2, there are very few equations in the text, and even those in Chapter 2 should be interpretable to readers with the equivalent of college-level algebra. I, with the help of my colleague Michael Mesterton-Gibbons, have made a conscious effort to write the text surrounding equations in such a way that even if one were forced to skip the math (and I would encourage everyone to at least give it a crack before moving on), the message makes its way through to the reader.

I would be remiss if I did not take a moment to mention early on why I do not have a chapter on cooperation in humans. I thought a great deal about writing such a chapter and vacillated, weighing the pros and cons. In the end, I decided against such a chapter. Once I delved deeply into the human cooperation literature, I realized that there are hundreds, if not thousands of experiments on cooperation in humans. But, this, in and of itself, would not be a sufficient cause to omit human studies from this book. Rather, the major problem I encountered was that almost none of these studies is presented in the light

of evolutionary theory (sad, but true) and so one would need to sift through all the literature and then reformulate it all in the context of evolutionary ideas. In addition, cooperation in humans has been studied in such a wide variety of contexts that it would likely be hard to make any generalizations across such studies, even if they could be presented in an evolutionary framework. Finally, it is often very unclear exactly what experimenters even meant by "cooperation" in a particular human study.

This book was written with advanced undergraduates, graduate students, and primary researchers in mind as the target audience. While I imagine that my audience will be primarily biologists, I sincerely hope that psychologists, anthropologists, and political scientists will consider this book for their classes (or book shelves) as well. These disciplines have had a profound impact on the study of cooperative behavior, but have often (though not always) ignored the evolutionary implications of their own work. If this book makes individuals in the above-mentioned disciplines realize that the evolutionary approach has much to offer, it will have performed a great service.