

*John Alcock*

# Animal Behavior

SIXTH EDITION



*Sixth Edition*  
**Animal  
Behavior**

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*AN EVOLUTIONARY APPROACH*

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### The Cover

Male *Telostylinus* flies in combat on a fallen mango tree in a Sulawesi rainforest. Males of this species engage in a resource-defense mating strategy (see Chapter 13), defending holes bored by beetle larvae which are attractive to female flies as egg-laying sites. The combatants rear up as high as possible on their long legs, pressing their heads together and pushing strenuously against each other, in a remarkable example of convergent evolution of threat displays; similar behavior has evolved independently in many other animals, including large vertebrates such as red deer (see Chapter 8). *Photograph by Ken Preston-Mafham/Premaphotos Wildlife.*

### The Frontispiece

An Adélie penguin rookery in Antarctica. Breeding grounds are carefully chosen by these birds based on several factors (see Chapter 11). *Photograph by Colin Monteath/Hedgehog House.*

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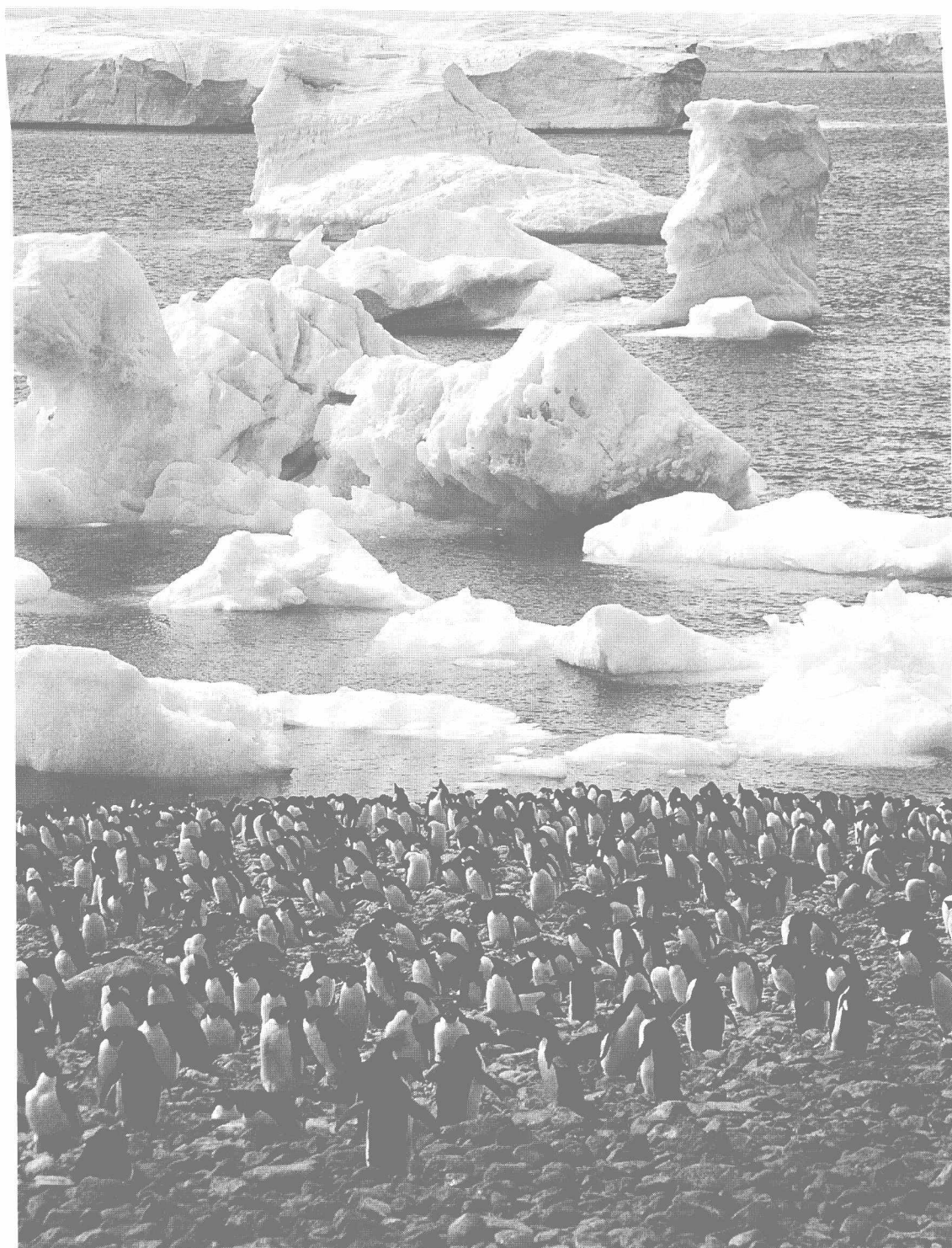
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# Animal Behavior



*With thanks to George C. Williams  
for explaining what evolutionary theory is*

# Preface

Another four years or so has passed since I last confronted my computer and stacks of animal behavior journals and reprints in an attempt to bring my textbook up to date while also making it a more effective educational tool. The job of revising is made both easier and harder by the exponential increase in the number and quality of research articles on behavior over the past four years. In the first edition of the book, I cited fewer than 500 scientific publications. I am now up to 1300, of which only a handful were used the first time around. I am not at risk of running out of new discoveries to report to my readers.

On the other hand, this flood of new information is hard to digest in a timely fashion. For example, a few days before writing this Preface, I came across a report in the journal *Nature* demonstrating that the very same genes that are responsible for the development of respiratory gill plates in wingless crustaceans are also present in insects, in which they are involved in the development of wings. This finding has considerable significance for our understanding of how insects came to fly, a topic that fascinates me. However, I found this paper too late to incorporate it into Chapter 7, having decided that if I did not stop adding new material I would never get done.

The task of picking and choosing among literally thousands of good papers forces me to select just a fraction of those I might use, after which I generally reduce a complex story to a line or two of text. Even so, it is a struggle to keep the book at a manageable length. A textbook need not be, and in fact should not be, an encyclopedia. Therefore, in revising, I have tried to keep the focus on the handful of really big ideas in behavioral biology: the distinction between different kinds of underlying causes of behavior, how natural selection theory is used to develop hypotheses on the evolutionary causes of behavior, what is meant by a cost–benefit approach to behavioral analysis, and most importantly, the procedures that scientists follow when trying to discriminate between competing explanations for something.

In order to achieve this goal, I have rewritten the book extensively, incorporating new evidence and new topics, such as the origins of insect flight, where it seemed appropriate. I have, however, retained the traditional organizational scheme of the book, except for one major change. In this edition, the second chapter no longer classifies behavior into instincts and the different kinds of learning, but instead presents the topic of communication to explain the various kinds of internal mechanisms, ranging from genes to neurons, that underlie animal behavior. The following chapters cover each of these mechanisms individually before the book switches gears with two chapters on the evolutionary bases of communication, again using this subject to preview a series of subsequent chapters. In these chapters, evolutionary theory is applied to topics ranging from antipredator to reproductive to social behav-

ior, and finally to human behavior as well. I would like my readers to come away understanding more about how animal behavior has been studied and why the logic of science is worth appreciating.

### *Acknowledgments*

As in all previous revisions, I received aid from many people. First, all the chapters in their initial revised drafts were read by one or more colleagues from the United States or Canada, including Luis Baptista, Martin Daly, Susan Foster, Steven Gaulin, Ann Hedrick, Ronald Hoy, Walter Koenig, Donald Kroodsmas, Steven Lima, Robert Montgomerie, Randy Nelson, David Queller, and Jon Waage. All these persons made a large number of suggestions for changes, most of which were clearly correct, and many of which I actually followed. Sometimes, however, laziness on my part, or incomprehension, or stubbornness prevented me from doing the right thing, and so needless to say I am responsible for any errors or shortcomings that remain in the text.

Many other behavioral biologists have assisted me by doing such things as sending me reprints, answering my questions, and responding to requests for photographs or permission to use their material in figures or diagrams. I have tried to acknowledge the permission givers at the appropriate illustration in the text. Acknowledgments to the publishers who have also generously granted permission to use their copyrighted material appear between the Bibliography and Index.

I also thank my editor Peter Farley at Sinauer Associates, where he (and I) have the help of Kerry Falvey and the other Sinauerians, as well as Norma Roche, a remarkably skillful copy editor who saved me from myself in many places in the text. Peter has effectively steered me through the complicated process of producing a manuscript for two editions now, and I continue to bless my lucky stars that I signed on with Sinauer Associates more than two decades ago.

Most authors need support from their family and friends if they are to remain sane, and here too I am fortunate. My wife Sue is amazingly tolerant, even to the point of becoming my unpaid executive field assistant on bee research projects in remote Western Australia. When we are in Arizona, my son Nick comes over to have dinner with us often, after which he and I play three games of ping-pong, one of which he manages to lose so that I will have reason to go on living. A group of politically dubious white male colleagues, including my department chair, Jim Collins, as well as Dave Brown, Stuart Fisher, Dave Pearson, and Ron Rutowski, often keep me company at lunch, where we discuss teaching, the shortcomings of others, and what it is like to grow old. On Friday afternoons, we sometimes wander over to the faculty club, having several years ago traded in large plastic pitchers of Budweiser and greasy french fries at the Chuck Box for small tapered glasses of Pilsner Urquell and delicate cheese-filled jalapeños at the club. There we discuss teaching, the shortcomings of others, and what it is like to grow old. As I grow older, I am increasingly grateful to my friends and family for the many pleasant distractions they provide in the intervals when I am not looking at a computer screen.





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## CHAPTER 1

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# *An Evolutionary Approach to Animal Behavior*

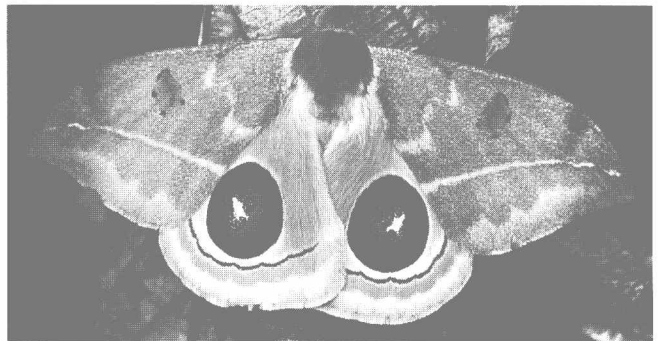
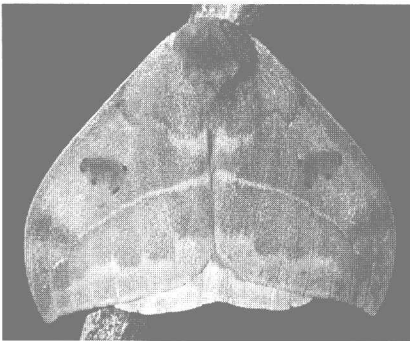
**F**OR HUNDREDS OF THOUSANDS OF YEARS, humans observed animals for a thoroughly practical reason: their lives depended on a knowledge of animal behavior. Even today, the study of animal behavior has great potential importance for our species. For example, understanding the reproductive behavior of agricultural pests may ultimately lead to their control, while a knowledge of the migratory routes of an endangered whale or shorebird may enable conservationists to design adequate reserves to save the animal from extinction. Even if there were absolutely no practical benefits to be gained from learning about animal behavior, the subject would still be worth exploring because it is so fascinating. Who would have guessed that praying mantises can detect the ultrasonic cries of



predatory bats, while Belding's ground squirrels treat their full siblings differently from their half-siblings, and male black-winged damselflies use their penises to scrub other males' sperm out of their mate's sperm storage organ before transferring their own sperm? In the pages ahead, you will learn about many other equally remarkable feats of animals. The point of this text, however, is not only to introduce you to these entertaining discoveries, but also to help you understand how scientists have determined that praying mantises can hear sounds inaudible to humans and have demonstrated that the penis is a weapon in the sperm competition wars among black-winged damselflies. This book is dedicated to the proposition that the process of doing science is every bit as interesting as the findings that are its end product. If I can help my readers understand the beautiful, useful logic of science, as well as appreciate the wonderful diversity of animal behavior, my textbook will have done its job.

## Questions about Behavior

I lived for one summer in Monteverde, a tiny community in the mountains of Costa Rica, and while I was there a friend loaned me a black light, which I hung up by a white sheet on the back porch of our home. The ultraviolet rays of the lamp attracted hundreds of moths each night, and many stayed on the sheet until I could inspect them. Some mornings I found a huge bright yellow moth of the genus *Automeris* clinging to the sheet. In the chilly dawn, the sluggish moth did not struggle if I picked it up carefully. But if I jostled it suddenly, or poked it sharply on its thorax, the moth abruptly lifted its forewings and held them up to expose its previously concealed hindwings. The hindwings were marvelously decorated, with



1 *Automeris* moth from Costa Rica. (Left) Moth in its resting position with forewings held over the hindwings. (Right) After being jabbed in the thorax, the moth pulls its forewings forward to expose the “eyes” on the hindwings. Photographs by (left) the author and (right) Michael Fogden.