ANIMAL BEHAVIOR

SEVENTH EDITION

JOHN ALCOCK

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AN EVOLUTIONARY APPROACH

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The Cover

A bugling elk conveys honest information about his fighting capacity to rival males. Photograph by Bruce Lyon.

The Frontispiece

The threat display of the Hamadryas baboon raises many questions for evolutionary biologists. Photograph by C. K. Lorenz.

Animal Behavior: An Evolutionary Approach, Seventh Edition

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Preface

Another four years or so have passed since the previous edition of Animal Behavior appeared. During this time, much that is depressing has occurred on the political and environmental fronts. Let us not dwell on these events, but instead consider the positive side of the ledger, which includes the many excellent papers on animal behavior that have been written over the last few years. Indeed, the rate at which important discoveries about behavior are being made has steadily increased throughout the lifetime of my textbook. Just pick up a recent copy of any journal in the discipline and compare the research reports there with those in the same journal 15 or 20 years previously. Thus, in 1982, the journal *Animal Behaviour* published 1264 pages of reports; in 2000 the total was 2180 pages, a figure that underestimates the actual increase because the journal substantially enlarged its page size in 1998. Moreover, the quality of the work, as well as its quantity, has changed. The average recent paper on animal behavior is more sophisticated and interesting than the average paper written in the 1980s. Scientists really do build on what others have accomplished, which sets the bar higher and higher each year.

As researchers have met the challenge of expanding our already substantial knowledge of animal behavior, they have generated an embarrassment of riches for a textbook writer. As I have revised my book again, my main difficulty has been what to leave out, not what to put in. Although there have always been many more good papers than space available for my summaries, this time around the problem has seemed especially acute, given the numbers of excellent research reports coupled with my desire to limit the length of my book. Despite efforts in the past to keep the number of pages of text under control, my book had grown bigger over the years. This time I have managed to reverse the trend, which should make the book's contents more digestible, although it does mean that some good stories were omitted. Readers of my book can, however, explore any behavioral topic of their choice by turning to the original literature. In this regard, one tool—the Web of Science (http://www.webofscience.com)—is tremendously valuable because it provides such an easy and quick way to track down the work of particular researchers and to follow the trail of papers that cite a research report of interest. I cannot recommend this search mechanism too strongly.

In addition to bringing the book up to date and reducing its length somewhat, I have been able to incorporate color illustrations throughout the text, thanks to the willingness of my publisher, Sinauer Associates, to make the move from black and white to full color. This change not only adds to the aesthetic value of the book, but should also help readers grasp the point of graphs more quickly and easily. The photographs may also help students see why so many behavioral biologists love studying real animals in real environments.

The many changes that I have made to this seventh edition of my book have all been made with one primary goal in mind: to help my readers see how researchers have been able to reach satisfactory conclusions about how and why animals do the things they do. I hope that its examples of the wonderfully interesting research done on animal behavior will make the point that scientific logic offers a powerful means to gain an understanding of nature.

Acknowledgments

The author of any textbook depends on cooperation from a surprisingly large number of people. As I have rewritten the book again, I have been very fortunate in having many generous colleagues willing to give me their time, advice, photographs, and other forms of help. Mike Maxwell was especially helpful in providing information on microsatellite analyses. All the chapters of the book have incorporated changes suggested to me by the following reviewers: Alex Basolo, Eliot Brenowitz, Ken Catania, Robin Dunbar, Bruce Lyon, Jim Marden, Bob Montgomerie, Randy Nelson, Gabrielle Nevitt, Don Owings, Steve Nowicki, Kern Reeve, Gene Robinson, Tom Seeley, Nancy Segal, David Westneat, and Jeanne Zeh. Special thanks to Bob Montgomerie for reading the entire manuscript and for offering extremely helpful suggestions about how to do things better.

A host of other colleagues have provided me with permission to use illustrations that originally appeared in their papers, and some have given me the illustrations themselves. I want to single out Bruce Lyon for special thanks; his superb photographs appear in many places throughout the text as well as on the cover of the book. I have acknowledged all suppliers of photographs in the text at the appropriate figures. Acknowledgments to the publishers who have also generously granted permission to use their copyrighted material appear on pages located between the Bibliography and the Index.

My editor at Sinauer Associates, Pete Farley, has done the hard and often unglamourous work of keeping the project moving ahead. I am very grateful to him as well as to all the other Sinauerians, especially Chelsea Holabird, Joan Gemme, Chris Small, David McIntyre, and Mara Silver. Norma Roche, who copyedited this edition as well as many others, really knows how to fix mistakes. Readers of my book are lucky that they get to read the copyedited version rather than the original draft.

Although chapter reviewers, photographers, editorial staff, and presidents of the United States often change from edition to edition, some things stay the same, which provides a certain reassuring stability to my life. My wife Sue continues to cope with my many idiosyncrasies, still listening thoughtfully whenever I vigorously denounce the likes of, say, Henry Kissinger or Antonin Scalia, still willing to live in a cramped campervan for months at a time when we are in Western Australia for another round of bee research. My younger son Nick is still in town (Tempe, Arizona), and he takes time off from helping those accused of driving under the influence to help us eat dinner and play ping-pong. As in the past, he lets me win once in a while so that I can retain some small measure of self-esteem, that most important of modern commodities. My older son Joe is close enough (Albuquerque, New Mexico) that he can join us on occasion, helping me maintain the illusion of being surrounded by family. In addition, I am happy to report that none of my friends at Arizona State (among them Dave Brown, Steve Carroll, Jim Collins, Stuart Fisher, Dave Pearson, and Ron Rutowski) has yet gone to his reward, which means that we can all get together at lunch and sometimes on Friday after-

noons for beer, just as we have been doing for decades. Admittedly, the amount of beer that we consume has changed, dropping from the pitcher per person of the good old days to a glass or two currently, but the topics under discussion (the numerous disadvantages of getting older and the troubles caused by defective colleagues) have remained the same, thank goodness. To my family and friends, thank you.

Contents in Brief

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1 An Evolutionary Approach to Animal Behavior

◀ ***Charles Darwin's study*** *in Down House where he developed the theory of evolution by natural selection, the foundation for the modern study of animal behavior. Photograph by Mark Moffett*

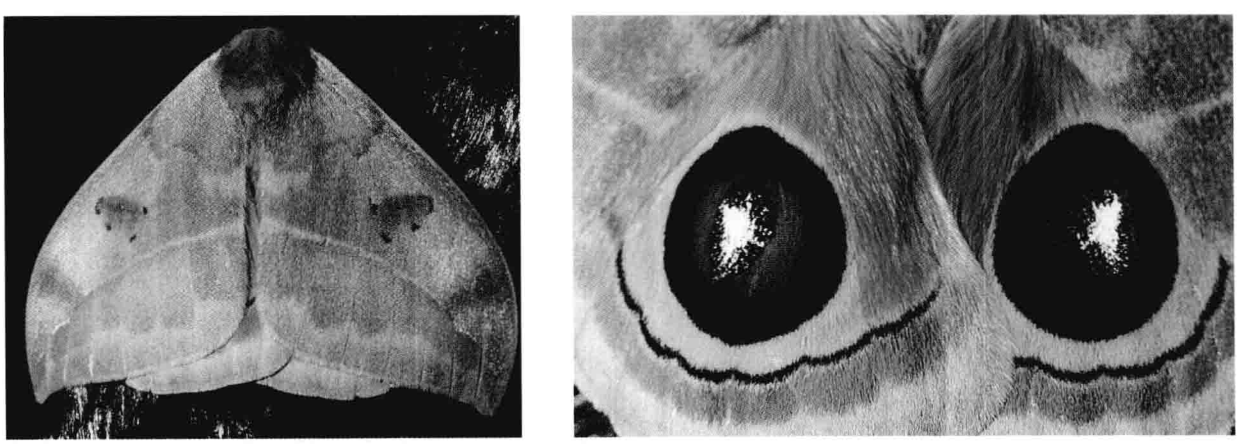
For hundreds of thousands of years, humans observed animals because their lives depended on a knowledge of animal behavior. Even today, the subject still has great practical significance. Information on the reproductive behavior of insect pests, for example, may ultimately lead to their control, while knowledge of the migratory routes of an endangered whale or shorebird may enable conservationists to design adequate reserves to save the animal from extinction. Moreover, an understanding of the evolutionary basis of our own behavior might help us identify why we so often damage our environments, perhaps enabling us to reduce our destructive tendencies [1251]. But even if the only beneficiaries of studies of animal behavior were the persons who conducted the research, I suspect that work in this field would continue. Learning how and why animals behave is an intrinsically fascinating business. Perhaps you can imagine what it would be like to be the first person to discover that male damselflies actually use their penis as a scrub brush to remove the sperm of rival males from their mates [1177]; or maybe you can put yourself in the shoes of the person who first showed that female Seychelles warblers could control the sex of their offspring so as to have daughters at times when it was most advantageous [641].

In the pages ahead, you will learn about these and many other remarkable discoveries. The point of this text, however, is not only to introduce you to these entertaining findings, but also to help you understand how scientists have determined that the damselfly penis serves as a competitive weapon of sorts or that the control of offspring sex ratio by the Seychelles warbler is an adaptation with a particular purpose. I believe that the process of doing science is every bit as interesting as the findings that are its end product. If I can help you understand the 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, which was founded by pacifist Quakers from the United States around the time of the Korean War. 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 belonging 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 circular patches that looked like two eyes, which seemed to stare back at me (Figure 1).

Anyone seeing *Automeris* abruptly expose its hindwing "eyes" will have some questions about the behavior. But no matter how long the list of questions, each query can be assigned to one of two fundamentally different categories: "how questions," about the **proximate** mechanisms inside the moth that cause the behavior, or "why questions," about the **ultimate** or evolutionary reasons for the behavior [774, 859]. "How questions" about behavior ask *how* an individual manages to carry out an activity; this category of questions requires explanations about how an animal's internal mechanisms developed and how



1 ***Automeris* moth from Costa Rica.** (Left) The moth in its resting position, with forewings held over the hindwings. (Right) After being jabbed in the thorax, the moth pulls its forewings forward, at which time the "eyes" on the hindwings become visible. Photographs by the author.

they then cause the animal to behave in a certain way. In contrast, "why questions" about behavior ask *why* the animal has evolved the mechanisms that underlie its actions.

How Questions about Proximate Causes

Consider the following questions about the wing-flipping reaction of an *Automeris* moth to a sharp poke:

- How do the moth's muscles make its wings move, and what controls those muscles?
- How does the moth know when it has been touched?
- Did the foods the moth ate as a caterpillar influence how it behaves as an adult?
- Did the moth inherit this behavior from its mother or father?

What these questions have in common, despite their diversity, is an interest in the operation of mechanisms *within* the moth that cause it to pull its forewings forward, revealing the amazing hindwings. The diversity of proximate questions is great enough, however, that we can subdivide them into two complementary groups, one dealing with the interactive effects of heredity and environment on the development of the mechanisms underlying wing-flipping, and the other dealing with how the fully developed physiological mechanisms actually operate when the behavior occurs.

The developmental side of the equation has to do with how the moth's heredity—its genes, its DNA—influenced the proliferation and specialization of cells that occurred as a fertilized egg gave rise to a caterpillar, which grew into an adult with a particular kind of nervous system. The operational side of the equation has to do with how neural mechanisms within the adult moth detect certain kinds of stimulation and how messages are then relayed to activate muscular reactions. Research on the developmental and physiological aspects of behavior remain to be carried out for *Automeris,* but someday we may learn about both of these proximate causes of its behavior.

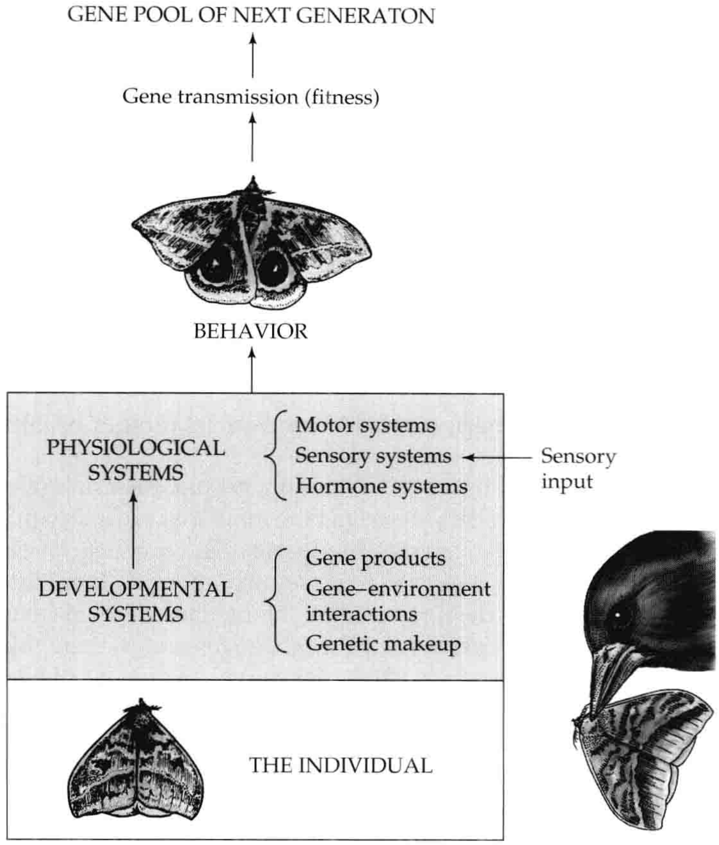
Why Questions about Ultimate Causes

Even if we already knew everything there was to know about the proximate causes of wing-flipping by *Automeris* moths, we could still ask many more questions:

- What do today's moths gain, if anything, by wing-flipping?
- Has the behavior changed over evolutionary time?
- If so, what were the predecessors of today's wing-flipping response?
- If the behavior has changed, what caused the changes?

These questions all involve the evolutionary, or ultimate, reasons why an animal does something. Why does the moth suddenly lift its wings and expose its eyespots when it is molested? The British scientist David Blest suggested that the action spread because in the past wing-flipping frightened off some bird predators when they mistook the moth's eyespots for the eyes of *their* enemy, predatory owls [116].

If Blest was right and wing-flipping behavior saved the lives of moths in the past, then the evolutionary process has contributed to the persistence of the proximate mechanisms that enable today's moths to behave the way they do. Particular genes present in the bodies of contemporary *Automeris* moths have been replicated and passed on from generation to generation, perhaps because they helped the moth develop an ability that frightened away predatory birds, enabling it to live long enough to transfer its hereditary informa-



2 Proximate and ultimate causes of behavior. At the proximate level, various internal mechanisms enable an *Automeris* moth to execute its wing-flipping behavior. At the ultimate level, the moth's reaction to bird predators determines its reproductive success, as measured by how many copies of its genes reach the next generation. Reproductive differences among individuals with different proximate mechanisms determine which genes are available to influence the development of individuals in the next generation.

tion to some descendants. This process could help explain why *Automeris* moths living in Monteverde today receive genes from their parents that promote the development of wing-flipping behavior. The developmental plan, and therefore the behavioral abilities, of each member of the species is a result of differences among individuals in their reproductive success over evolutionary time (Figure 2).

The current function of a behavior offers insight into its possible usefulness in the past, which could help explain why the trait spread and replaced others over time. Characteristics that currently advance the reproductive chances of individuals could plausibly have had the same effect in the past, thereby affecting the course of evolution. But what traits preceded the wing-flipping behavior of modern *Automeris?* If we could go back far enough in time, we would find an ancestor of the moth that did not exhibit the behavior. Perhaps the origins of wing-flipping involved wing movements associated with taking flight, movements that have been altered during the moth's history, just as the color pattern of the hindwings has certainly changed over time [115]. A full understanding of the ultimate causes of wing-flipping requires investigation into the initial form and subsequent evolution of the behavior, as well as the processes responsible for the changes.

You should now be able to discriminate proximate (mechanistic) questions from ultimate (evolutionary) ones (Table 1). If you wanted to find out how the nervous system of *Automeris* moths controls the wing-flipping response, you would be interested in the proximate basis of behavior, as is anyone concerned with how genetic, developmental, neural, or hormonal mechanisms work within an animal's body. On the other hand, if you were interested in whether wing-flipping evolved because of past predation pressure, you would be deal-

TABLE 1 Levels of analysis in the study of animal behavior

Proximate Causes	Ultimate Causes
1. Genetic–developmental mechanisms Effects of heredity on behavior Development of sensory–motor systems via gene–environment interactions 2. Sensory–motor mechanisms Nervous systems for the detection of environmental stimuli Hormone systems for adjusting responsiveness to environmental stimuli Skeletal–muscular systems for carrying out responses	1. Historical pathways leading to a current behavioral trait Events occurring over evolution from the origin of the trait to the present 2. Selective processes shaping the history of a behavioral trait Past and current usefulness of the behavior in promoting lifetime reproductive success

Sources: Holekamp and Sherman [532], Sherman [1046], and Tinbergen [1139]

ing with an ultimate issue, as is anyone who wants the answers to questions about the reproductive value of a trait and its historical foundations (see Figure 2).

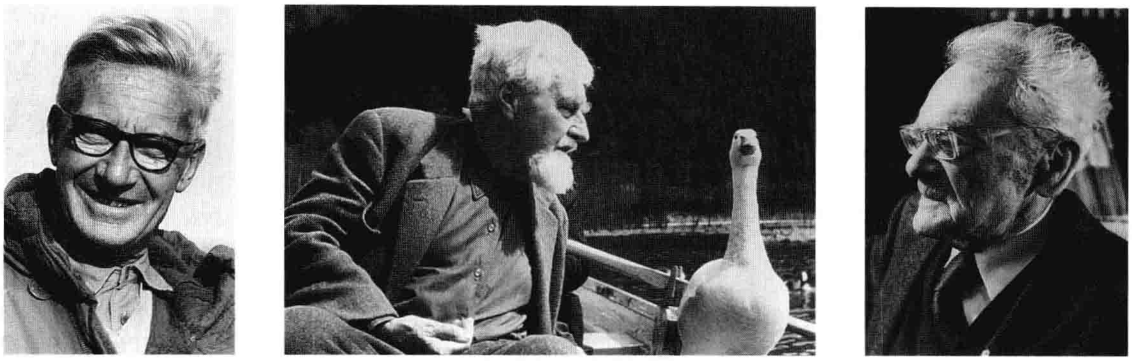
Moreover, if someone were to claim that work on the evolutionary basis of wing-flipping behavior eliminated the need to answer questions about the physiological basis of the behavior, you would (I hope) object strenuously. Proximate and ultimate hypotheses are complementary, not mutually exclusive—a concept that many people find difficult to grasp. For example, I once read that capuchin monkeys rub the oils from citrus fruits onto their fur because the chemicals may help heal skin wounds. The author then added, "Of course, the monkeys may simply enjoy the sensation," as if this explanation meant that we could ignore the medicinal benefit hypothesis. That would be a mistake. At a proximate level, monkeys may indeed derive pleasure from applying certain substances to their bodies, but this explanation does not replace the ultimate wound-healing hypothesis. If, in the past, monkeys that liked to rub citrus oils on their skin had even slightly greater reproductive success than individuals that were indifferent to oily sensations, we would better understand why all capuchins today use citrus oils in a particular fashion. The full analysis of any behavior involves answering both proximate *and* ultimate questions.

Answering Proximate and Ultimate Questions about Behavior

It is one thing to be curious about a mechanism of behavior or its evolutionary foundation and another thing to satisfy one's curiosity. Getting valid answers to biological questions requires a particular approach, called the **scientific method,** whose logic must be understood if you are to grasp why biologists accept some conclusions but not others. We shall explore this issue with examples taken from two studies done in the middle of the twentieth century by the great behavioral biologist Niko Tinbergen, one on a proximate question and the other on an ultimate one.

Beewolves and Homing Behavior

Tinbergen helped make the study of animal behavior a part of modern biology. Although Charles Darwin investigated earthworm burrowing behavior, bumblebee mating, bowerbird displays, and the facial expressions of dogs and



3 The founders of ethology. From left to right: Niko Tinbergen, Konrad Lorenz, and Karl von Frisch. Photographs by (left) B. Tschanz, (middle) Sybille Kalas, and (right) O. von Frisch.

humans, no scientific journals were devoted to behavioral research until the mid-1930s. At that time, the field of **ethology** originated under the guidance of Tinbergen, a native of the Netherlands, and his friend Konrad Lorenz, an Austrian. They and their colleagues investigated both proximate and ultimate questions about the behavior of gulls, jackdaws, butterflies, snow buntings, greylag geese, moth caterpillars, and many other animals in their natural environments [720, 1137]. These pioneering ethologists ultimately received the Nobel Prize in Medicine in 1973, which Tinbergen and Lorenz shared with Karl von Frisch (Figure 3), an Austrian researcher famous for his work on honey bee communication (see p. 220).

One of Tinbergen's earliest ethological studies began in 1929, more than 40 years before he was awarded the Nobel Prize, when he discovered a large number of digger wasps nesting in the sand dunes near Hulshorst, Holland. These wasps so fascinated Tinbergen that he and his fellow researchers spent weeks living in a primitive campsite and bicycling up to 70 miles a day in order to learn more about them [1137]. The species of digger wasp that caught Tinbergen's eye was *Philanthus triangulum*, the beewolf, so named because it captures and paralyzes honey bees by stinging them (Figure 4, left). Female beewolves transport captured bees to an underground nest, where they are stored in brood cells off the main tunnel. The bees are eventually eaten by the wasp's offspring when the little grub hatches out from an egg laid on a bee by the nesting female.

Some sand dunes in Hulshorst were dotted with hundreds of burrows, each marked with a low mound of yellow sand that the female beewolf had transported to the surface when excavating her nest. Tinbergen noted that when a beewolf left her burrow to go bee hunting, she covered up the opening by raking sand over it, hiding it from view, and yet when she came back a half hour or an hour later carrying a paralyzed honey bee, she darted directly to her hidden nest entrance, ignoring all the others (Figure 4, right). By giving females unique paint marks, Tinbergen verified that each wasp built and provisioned only one nest at a time.

The skill with which the marked beewolves found their hidden tunnels intrigued and puzzled Tinbergen. How could they get home so easily? The wasps provided a hint to a possible answer: when a female left her nest, particularly on her first flight of the day, she often took off slowly and looped over the nest, flying back and forth in arcs of ever-increasing length and height. After a few seconds, she abruptly turned and zipped off in a straight line (to the bee-hunting grounds, which were about a kilometer away). Tinbergen suspected that the wasps "actually took in the features of the burrow's surroundings while