



**S.A. BARNETT**

# **MODERN ETHOLOGY**

THE SCIENCE OF ANIMAL BEHAVIOR

# **MODERN ETHOLOGY**

THE SCIENCE OF ANIMAL BEHAVIOR

**S.A. BARNETT**

Australian National University

New York Oxford  
OXFORD UNIVERSITY PRESS

1981

Copyright © 1981 by Oxford University Press, Inc.

Library of Congress Cataloging in Publication Data

Barnett, Samuel Anthony.  
Modern ethology.

Bibliography: p.  
Includes index.

1. Animals, Habits and behavior of. I. Title.  
QL751.B1865 591.51 80-12473  
ISBN 0-19-502780-9

Cover photo: N. Tinbergen

Printed in the United States of America

# PREFACE

To write a book, . . . can be a "vital joy", but a joy which is inevitably united with the thorns of anxious care. It is not a contribution to perfection. . . . To write anything worth writing is to arouse opposition, controversy . . .

John Passmore  
*The Perfectibility of Man*

More than a million species of animals have been named. The behavior of some thousands, from Protozoa to Primates, has been described in detail. The descriptions appear in tens of thousands of papers and monographs, of which most have been published since 1950. During this period the theories of ethology have gone through a complete upheaval.

In this book I try to give an orderly account of the most important findings in ethology. I define ethology as the science of animal behavior. The word has then the same status as "ecology" or "genetics": it denotes a major subdivision of biology. I do not limit ethology to study by a particular method, or to social interactions, or to the views of a single school; and four chapters on "learning" (part III) are largely based on the work of experimental psychologists. I hope the book will be used

by undergraduates and young graduates, and by their teachers, in all kinds of study of behavioral science.

In parts II, III, and IV behavior is classified mainly by its functions. Within chapters or sections the examples are sometimes arranged taxonomically. Certain examples could have been put in any one of several chapters. For instance, reproductive behavior is described in chapter 9, but it also appears in chapters 17 and 18. Similarly, bird song is discussed in chapter 12, before the general topic of communication is reached in chapter 13. There is no long segment of the book on the physiology of behavior, despite its importance; instead, physiological topics appear in many chapters. Nor is there a separate discussion of ecology and behavior; but ecological relationships turn up throughout the book. Other arrangements could have been used, but this one seemed the most convenient.

Most recent writings on ethology contain echoes of theories or concepts that are going out of use. These, and the ideas that are replacing them, are mentioned in many places; but the theoretical foundation of ethology is discussed mainly in chapters 16 through 19. This involves some repetition, which

is deliberate. The fragments of the history of ethology, given especially in chapters 17 and 18, will, I hope, help to guide readers through important writings that use concepts we are now giving up.

Among the many matters of debate, three are important in all branches of biology. No account of modern ethology is complete without them. First is the question of heredity and environment. This subject not only causes violent argument in its application to human beings: it is also a source of confusion even when no social implications arise. It presents severe conceptual difficulties that I try to meet especially in chapters 16 and 17: these chapters give an epigenetic account of the development of behavior, in which the interaction of nature and nurture is analyzed.

Second, there is the question of reductionism: should we expect eventually to reduce all behavior to physiology (and physiology, in turn, to chemistry . . .)? In this book I treat both analysis at the behavioral level and also "reduction" to physiology as essential: neither can replace the other.

Third and last, the fact of evolution and the theory of natural selection are part of the foundation of ethology. Emphasis on evolution is sometimes thought to be in conflict with an epigenetic interpretation, but in fact the two themes are complementary. At the same time, the role of evolutionary ideas in ethology needs to be examined critically. I try to meet this need in chapter 18.

There is much debate also on whether a "human ethology" is possible. Students are often confused about this, with good reason. Part V is therefore on the human species, and there I try to give clear statements on questions of method. Readers interested only in conventional ethology should skip this part; but those concerned with the relationships of ethology with other disciplines will probably concentrate on chapters 8 and 14–19. Human

behavior is also mentioned in other places in the book, whenever ethological methods seem to bear on human problems.

When there are rapid changes of ideas, there are also alterations in the meanings of words. Terms such as territory, dominance, imprinting, and habituation are used in different ways in different publications. I have tried to provide unambiguous and convenient definitions of all key terms, and to stick to the definitions throughout the book. These terms, and some others in common use that I do not recommend, are listed in the glossary.

One result of emphasizing definitions is that one becomes an easy target for adverse comment. I have been taken to task for using words, such as concomitant, propensity, and even orientation, without defining them. But these words are used with their ordinary meanings, given in any dictionary. The object of carefully defining key terms is to avoid ambiguity and obscurity.

Most of the work cited has appeared since 1950, but few items dated later than 1978 have been included. Nearly every section has references to recent reviews that give full information on sources. But many passages describe single researches: a reference is then given to the primary source—usually, a paper in a journal. Whenever an author's name is mentioned in the text or in a caption, there is a corresponding entry in the bibliography. Dates are given only when an author has more than one entry.

A textbook can be treated as a source of facts. This one contains many facts, some very strange. But studying a new subject can also lead to new attitudes. Some readers will perhaps appreciate, more than before, the variety and fascination of the ways in which animals live, and will have their curiosity further aroused. They may then be led to apply for themselves the scientific methods used to learn about behavior.

## ACKNOWLEDGMENTS

This book was made possible by my wife, Kate Munro; and my son Amos (born 1975) provided both an additional incentive and much stimulation. It is dedicated to them.

Sabbatical leave granted by the Australian National University allowed periods of uninterrupted work, for which I am most grateful.

In the mechanics of producing the book I had essential help from Anne F. Cook, Cathy E. McKay, and Marian Obenchain; and with the illustrations, especially photographs, from Ivan A. Fox. Others who kindly sent photographs or original drawings are acknowledged in the captions.

A number of altruistic friends and colleagues read and criticized substantial parts of the book: Valerie A. Brown, Hiram Caton, Marian Dawkins, J. Derek Freeman, John B. Gibson, Donald L. Gunn, Jeremy G. M. Robertson, Richard J. Wallace, Martin J. Wells. Among others who helped with special problems are: Michael V. Brian, Vincent G. Dethier, Robert M. W. Dixon, B. M. Fitzgerald, H. J. Frith, Madhav Gadgil, H. W. Levi, Geoffrey V. T. Matthews, Anne McLaren, Randolph Menzel, D. John Mulvaney, Philip J. Regal, Susan C. Wilson.

*Canberra  
April 1980*

S.A.B.

I should not like my writing to spare other people the trouble of thinking. But, if possible, to stimulate someone to thoughts of his own.

Ludwig Wittgenstein  
*Philosophical Investigations*

# CONTENTS

## I INTRODUCTION

### 1 The Science of Behavior 3

Questions of Method 3

The Evolutionary Framework 11

Breathing 94

Thermoregulation 96

Drinking 100

Feeding 101

Summing Up 118

## II MAINTENANCE

### 2 Movement and Orientation 15

Place and Time 15

Orientations Classified 22

The Senses and Orientation 33

Bird Migration 46

Summing Up 55

### 3 Predation and Protection 57

Types of Interaction between Species 57

The Variety of Predators 57

Predatory Searching 70

Crypsis 76

Aposematism 85

Deimatic Effects 89

Hunters and Hunted: Summing Up 91

### 4 Homeostasis and Behavior 93

The Concept of Homeostasis 93

## III ADAPTING TO CIRCUMSTANCES

### 5 Reflex Behavior 123

Reflexes 123

Habituation 129

Sensitization 139

The Problem of the Protozoa 143

Conditional Reflexes 146

### 6 Trial, Error, and Success 157

Experimental Methods 157

The Analysis of Trial and Error 163

### 7 Trial and Error in the Animal Kingdom 173

Turbellaria 173

Echinodermata 173

Oligochaeta 174

Insecta 175

Cephalopoda 182

Fish 189  
Birds 194  
Achievements and Constraints 195

## 8 Exploring, Improvising, and Imitating 201

Activity and Exploration 201  
Learning Set 222  
Apes and Language 229  
Social Influences 232  
The Concept of Learning 244

## IV SOCIAL CONDUCT

### 9 Courtship and Parenthood 249

Arthropods 249  
Fish 261  
Birds 266  
Mammals 279  
Summing Up 290

### 10 Grouping and Dispersion 293

Terminology 293  
Groups 296  
Special Cases of Cooperation 302  
Territory 306  
Crowding and Social Stress 334  
"Aggression" 344

### 11 Primate Groups 353

The Peculiarities of Primates 353  
Some Case Histories 354  
Status 372  
Occupied Regions 378  
Social Ethology So Far 380

### 12 The Ontogeny of Social Conduct 383

The Importance of Ontogeny 383

The Audible Signals of Birds 384  
Imprinting 395  
Primates 406  
Social Ontogeny 413

### 13 Analysis of Communication 415

The Concept 415  
The Sensory Modalities 416  
Signals and Displays 437  
Summing Up 450

## V THE HUMAN SPECIES

### 14 The Paragon 455

*Homo Sapiens* as a Primate 455  
Questions of Method 463  
Infant Development and Nonverbal Communication 466  
People As Animals 477

### 15 The Riddle

Human Diversity 479  
Language 482  
Models 486  
Classifying Knowledge 497  
Conclusion 502

## VI CONCEPTS

### 16 Variation and Heredity 507

Some Examples 507  
Genotype and Environment 516  
Applications to Human Populations 526  
Summing Up 534

### 17 The Concepts of Instinct 537

Some Traditional Notions 537  
Patterns of Behavior 544

Ontogeny and Environment 567  
The End of Instinct 575

## 18 Evolution and Ethology 579

Phylogeny and Order 579  
Natural Selection 583  
Niches of Extant Species 597  
Strategies of Reproduction 603  
Origins of Signals 613  
Functions of Signals 617  
Summing Up 618

## 19 The Concept of Behavior 621

Objectivity 621  
Evolution and Epigenesis 627  
Order and Diversity 629

Glossary 631

References 637

Index of Authors 681

Subject Index 691



# INTRODUCTION





# THE SCIENCE OF BEHAVIOR

I try to act and think on the hypothesis that all happenings are in principle explicable, and that, in so far as they are not completely explicable, this is because they consist of too many details for a human mind to grasp, and not because either the details or their pattern are beyond the scope of human reason.

J. B. S. Haldane (1963)

The science of animal behavior has special attractions, but it also puts unusual demands on our understanding. Everyday speech includes presumptions about animals which, for scientific analysis, have to be discarded. It is natural to say of a captive animal that it wants freedom. Or, if an adult animal exposes itself to danger through caring for a young one, we may exclaim at such self-sacrifice or altruism. And when a pest contrives to remain alive, despite efforts to kill it, we may remark on its intelligence.

All such ways of speaking can hinder understanding. All are examples of anthropomorphism, or of assuming that animals may be adequately described as if they had human needs, feelings, or abilities. Here are some examples of behavior explicable only if we discard such presumptions.

## 1.1 QUESTIONS OF METHOD

### 1.1.1 Needs and Feelings

The first concerns a herd of roe deer, *Capreolus capreolus*, kept in a paddock in a Swiss zoological garden. H. Hediger describes how a gate was carelessly left open, and the deer disappeared into a nearby forest where others of their species already lived. They had therefore escaped into an environment in which they could easily survive. Yet, soon afterward, the herd returned to the paddock. In human terms, it was as though prisoners, after making their escape, voluntarily returned to captivity. How can we explain this odd behavior? Here are some suggestions. Many mammals live in a well-defined region to which they cling as long as it provides needs such as food, shelter, and companionship. The return of the deer may be classified as an example of an attachment to a particular (satisfactory) region. We may also suspect that the habit of feeding in the paddock had some influence. If so, what induced the herd to move out? A possible answer is that the animals were exploring. Despite their attachment to an area, many animals are also

exploratory: they range quite widely, even though they regularly return to a home or center.

A critical reader will notice that these “explanations” are all hypothetical: they suggest reasons for the behavior observed, but provide no evidence. Such a reader may also have thought of additional hypotheses. For example, the deer may have been driven from the forest by the herd already in occupation. (If so, this would be an example of territorial behavior.) To account fully for what happened, experiments would be needed. But in this case no appropriate experiments were carried out. Hence all we can do is to propose explanations that seem likely from our general knowledge of animals.

Any person interested in animals is likely to observe or to hear of similarly strange and unexpected acts. Fortunately, some have been quite fully analyzed. Of all species, the honey bee, *Apis mellifera*, is among the most intensively studied (C. G. Butler; K. von Frisch, 1967; M. Lindauer, 1961; C. R. Ribbands). This animal is elaborately social, and has inevitably been described in human terms. In each colony one bee is larger than the rest and is surrounded by a number of attendants (figure 1-1). It was accordingly called the king. In Shakespeare’s *Henry V* an archbishop says:

They have a king and officers of sorts;  
Where some, like magistrates, correct at home,  
Others, like merchants, venture trade abroad,  
Others, like soldiers, arméd in their stings,  
Make boot upon the summer’s velvet buds.

But in the 17th century it was noticed that the king lays eggs. She therefore came to be called the queen. She is, however, not much like a human queen: she is the only fertile female, and all the other bees in the colony are her offspring.

This instance of anthropomorphic terminology is in itself harmless: nobody is misled by it. The

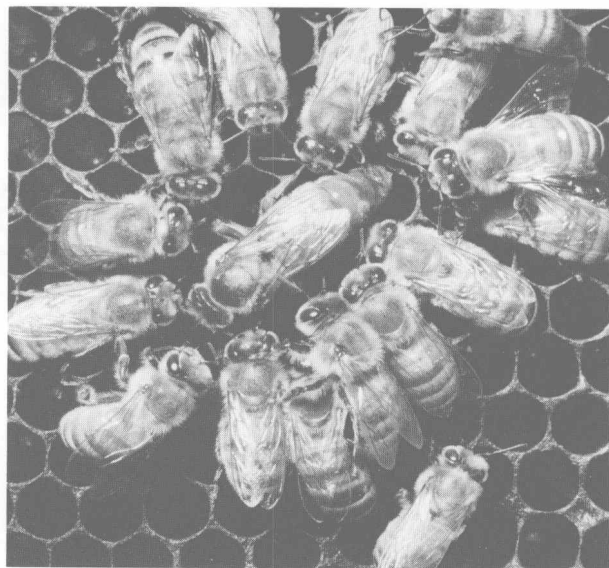


FIGURE 1-1 Queen bee, *Apis mellifera*, on a comb and surrounded by a group of workers. She secretes odorous substances that attract workers and impel them to feed her. (Courtesy Norman E. Gary)

same applies to a statement, published in 1823 and quoted by Frisch, that bees sometimes “indulge in certain pleasures and jollity, and . . . at times they even set about a certain dance after their fashion.” But such statements imply presumptions that can interfere with understanding. If the queen is removed from her colony, the conduct of the others gradually becomes disorganized. The change can be detected by an altered buzzing sound. In the 19th century, one observer wrote of the “low, mournful lament” of the bees deprived of their monarch. In contrast, modern experimental methods have told us something of how the change comes about. If a queen is isolated in a miniature cage, inside the hive, and the workers can touch her with their antennae and mouth parts, no such

disturbance occurs. Further experiment reveals secretions from the queen bee that are passed on among the workers and regulate their behavior. The best known of these chemical agents, queen substance, *trans*-9-keto-2-decenoic acid, not only ensures ordered behavior by the workers but also prevents the workers from developing ovaries. Only queens and the males (drones) have functioning gonads.

Accurate information on bee societies has been gained by painstaking observation and the use of quantitative methods from the physical sciences. For some purposes, even when we are concerned with behavior, it is convenient to treat an animal as a chemical system. Many advances in the understanding of behavior have depended on applying such methods. The result is an account often of marvels, but one that is detached, objective, and perhaps, to a newcomer to science, disconcerting. A description in more familiar terms is often more readable. Indeed, a leading entomologist, E. O. Wilson (1975), describes the role of a queen bee as a "gentle despotism"; and he writes of the "selfless" contribution of the workers to the upkeep of the colony. In another passage, on ants of the genus *Pheidole*, in which there are several "castes" (another well established anthropomorphism), he contrasts "the brutish soldiers . . . distinguished by an extremely limited repertoire of responses, and their versatile, nimble nestmates of the minor worker subcaste." Such expressions can make scientific writing more readable. One hopes that readers do not take them seriously.

Insects are so remote from ourselves that it is easy to reject the notion of a queen bee as a bossy female. Greater difficulties arise when we are dealing with domestic animals. Here, adopting a matter-of-fact attitude can produce unexpected conclusions. In Britain, under the law on "vivisection",

animals may not see other animals being killed. The attribution of human feelings to laboratory animals is obvious. It is also, at least for some species, inappropriate. Nobody who has dealt with laboratory rats or mice can suppose that the death of a rat or mouse under an anesthetic would have any significance for other rats or mice. (The dead body, however, would have significance: given the chance, the survivors would probably eat it.)

This is an example of the way in which good intentions are ill directed in the absence of knowledge. But, when we face questions of animal welfare, there are great problems in acquiring the necessary knowledge. We cannot ask an animal, as we would a human being, what it likes or dislikes. Or, at least, we cannot do so by verbal means. As Marian Dawkins (1977) shows, there is at least one kind of procedure by which we can, in effect, ask questions of animals. She is concerned with the confinement of hens in battery cages. Such cages look cruel: the hens are shut up permanently in a small space, and they can do little more than eat, drink, sleep, and lay eggs. Some hens were therefore given continuous access both to a commercial battery cage and to a large pen: the hens showed no preference. But other hens, allowed access to an outside hen run, preferred the run to a cage; this preference, however, was much influenced by the previous experience of the hens. In this rather unusual study the methods of experimental ethology are applied to a question concerning humane treatment of domestic animals.

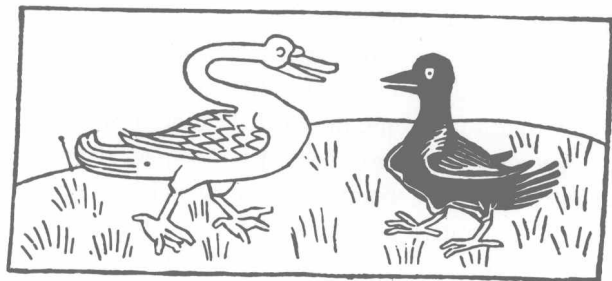
In general, the confinement of wild or domestic animals in cages, pens, or other enclosures raises many questions, some of which I mention above in the account of the roe deer that escaped. To us a cage is a prison—something from which to escape. Yet for a captive animal it may be a home and a refuge. When my colleagues and I were studying

confined colonies of wild rats, *Rattus norvegicus*, the members of one group gnawed their way through a concrete floor and escaped into a neighboring farm. There they caused us some embarrassment by killing and eating the chickens. But they regularly returned to their proper home; and, by choosing the right moment for blocking the escape tunnel, we were able to confine them all again. Many mammals and birds occupy well-defined regions, each of which constitutes in itself a kind of prison; but occupation is unforced, and removal may even be resisted. Our own preferences are not a reliable guide to what is good for other species.

### 1.1.2 Morals

Expressions such as “brutish soldiers”, applied to ants, remind us that throughout history animals have been used as examples of moral rather than scientific laws. The fables of Aesop and the bestiaries of the Middle Ages (figure 1-2) are well-known. Modern writers have maintained the tradition. Rudyard Kipling (1860–1939) wrote an entertaining short story, “The Mother Hive”, in

FIGURE 1-2 Animals as a source of moral instruction. A white goose (*Anser*?) exhorts a black bird (species uncertain). (After the *Dialogus Creaturarum*; from W. Ley, *Dawn of Zoology*, 1968)



which a colony of bees becomes infested with parasites. Although Kipling draws on his experience as a beekeeper, his story is presented as fiction. The parasites (which include the wax moth) are not put forward as examples of ecological relationships, but as agents of moral degeneracy.

Here, to compare with Kipling's fantasy, is an account of an actual nest parasite, studied by Bert Hölldobler (1969, 1970). Beetles of the genus *Atemeles* live in and on colonies of ants, *Formica* (figure 1-3). The beetles find the ants by moving around until they detect the odor of an ant colony. They then move upwind, and so reach their target. At the nest entrance a beetle must first present an ant worker with secretions from an “appeasement gland” at the tip of the abdomen. The ant feeds on the secretion, and seems to become tranquilized. The ant then refreshes itself from the “adoption glands” further forward on the abdomen, after which it usually carries the beetle into its nest. Inside the nest the beetle is fed by the ants; it stimulates them to regurgitate food, as if to a fellow ant, by providing tactile stimuli like those used by the ants among themselves. Such experimental findings make strange ways of living still more fascinating; at the same time, they leave moral issues where they belong, in human society.

Nonetheless, few of us can resist resemblances to man in other species. Figure 1-4 shows how a female hornbill, *Buceros rhinoceros*, is confined to her nest during the breeding season, while the male feeds her through a hole. In the past the wall has been assumed to be an analog of that surrounding a harem; hence the cock bird has seemed to be an extreme example of male chauvinism. But actual observation has shown the wall to be built by the female (Hugh Whistler). The reader is free to devise her or his own analogy for that.

People have a tendency to project not only their

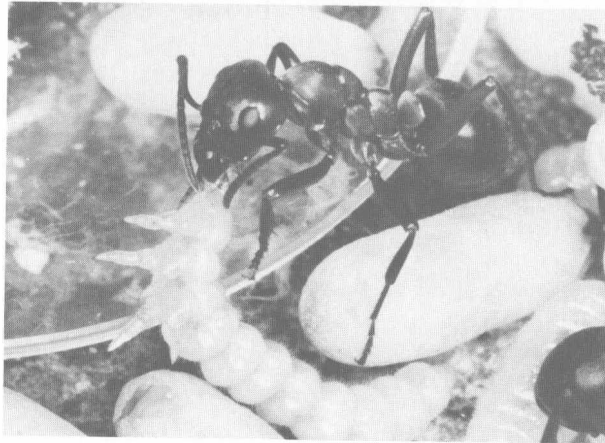
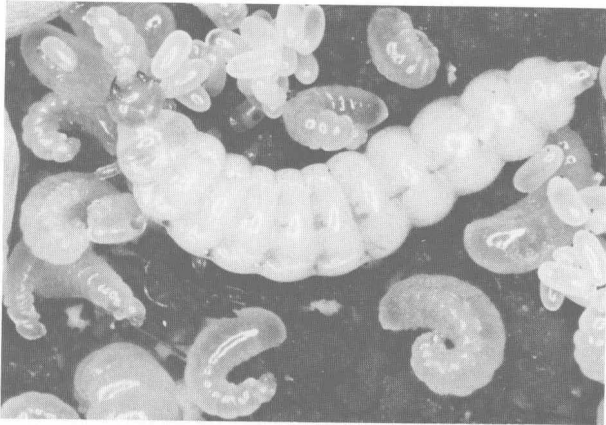


FIGURE 1-3 Above, the larva of a beetle, *Atemeles pubicollis*, feeds on the larvae of an ant, of the genus, *Formica*, in whose nest it lives. Below, an adult ant, instead of destroying the parasite, feeds it as if it were a larva of its own species. The beetle evidently has an odor which resembles that of an ant larva. (Turid Hölldobler)

moral principles onto other species, but also human impulses which they dislike. As Vernon Reynolds (1967) shows, our nearest relatives, the Primates, are convenient for this purpose. G. L. Buffon (1717–1789) gives a dramatic account of the ferocity and passionate nature of apes, which lead

them (he says) to kill every male Negro they meet and to abduct every woman (figure 1-5). Here, in contrast, is a terrifying incident recorded by a modern observer. A full-grown chimpanzee charged straight toward him; it came to within a few meters, suddenly stopped, picked up a young chimpanzee, and rushed off again.

Some writers give the impression that the moral principles that bind human societies apply directly to the social conduct of other species. Human beings are often altruistic: they choose to act in ways that benefit others even at a cost to themselves. To

FIGURE 1-4 The mating system of a hornbill, *Buceros rhinoceros*: the female is walled up in a tree while she lays her eggs, and the male feeds her through a narrow hole. Is this an analog of extreme male chauvinism? (Drawing copyright © 1974 by Turid Hölldobler. Reproduced from *Animal Architecture* by K. von Frisch by permission of Harcourt Brace Jovanovich, Inc.)

