John Alcock

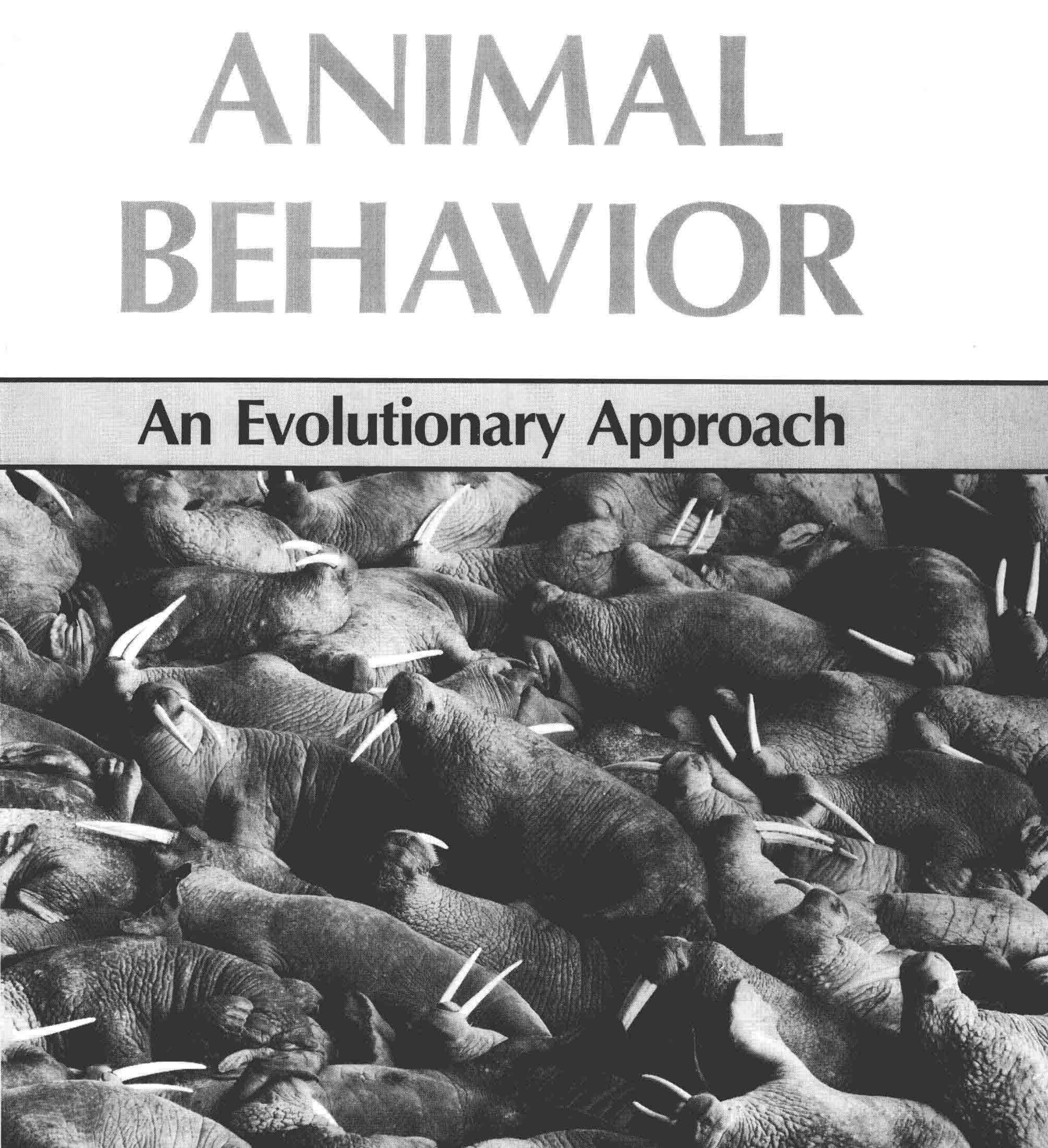
ANIMAL BEHAVIOR

FIFTH EDITION

JOHN ALCOCK
ARIZONA STATE UNIVERSITY

ANIMAL BEHAVIOR

An Evolutionary Approach



THE COVER

Pronghorn antelope, Wyoming. Photograph by Charles Krebs.

THE FRONTISPIECE

Walrus, Round Island, Alaska. Photograph by Charles Krebs.

Library of Congress Cataloging-in-Publication Data
Alcock, John, 1942–
Animal behavior: an evolutionary approach / John Alcock.—5th ed.
p. cm.
Includes bibliographical references and index.
ISBN 0-87893-017-5
1. Animal behavior. 2. Behavior evolution. I. Title.
QL751.A58 1993
591.51—dc20 92-39692
CIP

Printed in U.S.A.

8 7 6 5 4 3 2

Preface

I recently compared the first edition of my textbook with this fifth revision of *Animal Behavior.* No one would have any difficulty seeing that they had been written by the same person, even if my name were removed from the cover. The organizational scheme is fundamentally the same, some of the original illustrations have survived to the present, and much of the original intent remains intact. When I first set out to write this textbook, my goal was to demonstrate how researchers have used evolutionary theory to gain insight into why animals behave as they do.

This is still one of my central goals, but my book has also changed considerably from the first edition. In particular, over the years I have given ever-increasing weight to showing how scientists do science by testing alternative explanations, rather than simply presenting the "facts" derived from behavioral research. The conclusions of scientists often change and evolve, but the basic procedures they use have not changed appreciably over the past two decades, nor are they likely to change much in the next two decades. The process works, and I would like my book to help students understand what it is and why it deserves our enthusiasm.

This fifth version of *Animal Behavior* continues the evolution of the text toward an analysis of the process of doing science in the context of studying behavior. I have continued to add examples of studies that singly or together provide competing explanations for something intriguing in the world of animal behavior, studies that offer evidence that helps us evaluate the competing hypotheses. There is no shortage of such research in the ever-expanding literature on behavior. This edition contains citations for more than 1000 references; the first edition had half as many. I could have discussed 2000 research articles of quality were it not for the limitations of time, space, and my brain's capacity to remember what I have just read.

In addition to updating the material discussed in the text, I have formed a new chapter on animal communication. I have moved the chapter on parental care so that it follows the chapters on reproductive behavior and precedes the chapter on social behavior. And I have rewritten each and every chapter, making changes in content and organization that I hope will help my readers keep the big issues in mind. If the revisions I have made are productive ones, my readers will more readily see that there are only a few really big concepts that inform our view of specific problems and puzzles. I hope some students will carry these ideas away from a course, remember them past the final exam, and even put them to use occasionally when thinking about the wonderful natural world around us.

ACKNOWLEDGMENTS

To provide a general framework for this revision, the entire preceding edition was scrutinized critically by Charles Snowdon and Jon Waage. On the basis of their suggestions, I rewrote the text. Various chapters of the first version of the fifth edition were then reviewed by Luis Baptista, Eliot Brenowitz, Charles Brown, Martin Daly, Paul Ewald, Steven Gaulin, Erick Greene, Darryl Gwynne, Ann Hedrick, Walter Koenig, Donald Kroodsma, Robert Montgomerie, Randy Nelson, John Ringo, and Margo Wilson. I am grateful to these colleagues, all of whom know the meaning of the phrase "constructive criticism." My book is much the better for their efforts.

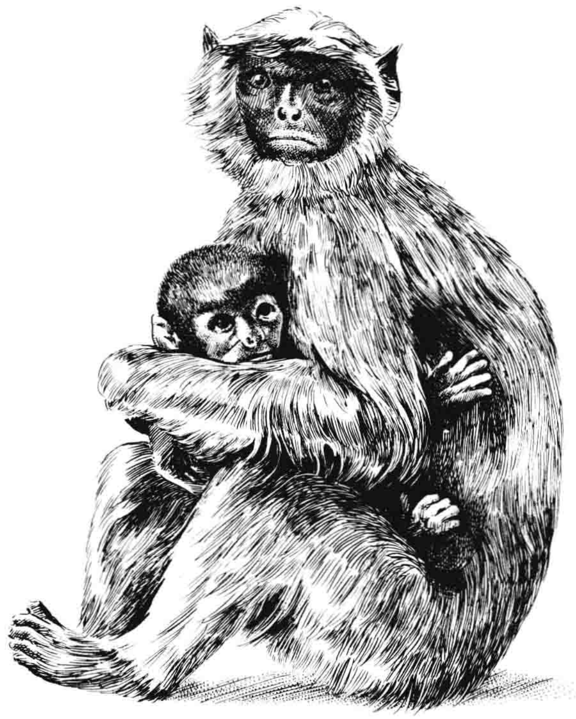
I would like to especially thank Jon Waage, whose exceptionally detailed criticisms and suggestions had great effect on the path I followed in revising the book this time.

Of course, I have also cheerfully ignored any uncongenial suggestions, and doubtless many imperfections and some outright errors still remain in this edition for which I alone bear full responsibility (here at last is a statement that none of my reviewers is likely to challenge).

Many other people and publishing concerns have helped by providing illustrations and permissions. I acknowledge these individuals either in the caption of the appropriate figure or in the illustration credits section. Special thanks are also due to Greg Ball and Marc Breedlove for their helpful suggestions on Figure 4-3.

My new editor at Sinauer Associates, Peter Farley, and his assistant Kathaleen Emerson, have taken over where Carlton Brose left off, helping me deal with the thousand and one details associated with writing a book. While I attended to these details, I also had the good luck to have James Collins as my departmental chairman at Arizona State University, where I hang out. He has calmly administered departmental life, leaving me free to be chained to my computer rewriting what I have already rewritten. At times, I teach classes of undergraduates, an experience that is as educational for me as for them. And various colleagues, a rapidly aging but still reasonably alert group of white middle-class males, also help keep me on my toes. The same goes for my wife, Sue, and sons Joe and Nick, who although they are no longer living at home nevertheless come back at times to help us figure out how to use the VCR and to make automotive suggestions. To one and all, thanks.

JOHN ALCOCK



For hundreds of thousands of years, humans observed animals for a thoroughly practical reason: their lives depended on a knowledge of animal behavior. Even today many useful things can come from studying this subject. For example, an understanding of the reproductive behavior of agricultural insect pests may help control them, while a knowledge of the migrating patterns of an endangered species may enable conservationists to design adequate reserves to save the animal from extinction. But even if there were absolutely no practical benefits to be derived from the study of animal behavior, the topic would still be worth learning about for the simple reason that it is fascinating. Animals are capable of extraordinary feats. Praying mantises can detect the ultrasonic cries of predatory bats. Ground squirrels treat their full siblings differently than their half-siblings. Some male damselflies use their penises to scrub other males' sperm out of their mate's sperm storage organ before transferring their own sperm. I am impressed by these and many other discoveries about the behavior of the creatures that share our world with us, and I hope that you will be similarly impressed. The point of this text, however, is not only to introduce you to these entertaining discoveries but also to help you understand how scientists go about investigating animal behavior. Learning how to think in a scientific manner has shaped the way I approach almost every issue in my life, not just my scientific research. This book is dedicated to the proposition that the process of doing science is every bit as interesting as the discoveries that are the end product of the process.

Contents

Preface xii

1 An Evolutionary Approach to Animal Behavior 1

Questions about Behavior 1
HOW QUESTIONS 2
WHY QUESTIONS 3
Evolutionary Theory and Behavior 6
DARWINIAN LOGIC AND THE STUDY OF BEHAVIOR 9
THE PROBLEM WITH GROUP SELECTION 10
The Science of Testing Hypotheses 12
TESTING ALTERNATIVE HYPOTHESES 13
TESTING HYPOTHESES ON INFANTICIDE 15
CERTAINTY AND SCIENCE 18

2 The Diversity of Behavior 23

Instincts 23
ETHOLOGY AND INSTINCTS 25
CODE BREAKERS 27
Learning 28
SPATIAL LEARNING 30
Misconceptions About Instincts and Learning 34
INSTINCTS CAN BE MODIFIED BY EXPERIENCE 35
BIASED LEARNING 37
LEARNED KIN DISCRIMINATION 39
LANGUAGE LEARNING 42
SPECIAL FEATURES OF ALL FORMS OF LEARNING 45
PROGRESS IN SCIENCE 46
The Evolutionary Basis of Behavioral Diversity 47
THE BENEFITS OF BIASED LEARNING 50

3 The Genetics of Behavior 57

Genes and Behavior: The Connection 57
GENETIC DIFFERENCES AND BEHAVIORAL DIFFERENCES 58
BEHAVIORAL DIFFERENCES CAUSED BY SINGLE-GENE DIFFERENCES 60
TESTING THE GENETIC DIFFERENCE HYPOTHESIS: TWIN STUDIES 68
GENETIC DIFFERENCES AND IQ DIFFERENCES 72
WHY IQ IS NOT "GENETICALLY DETERMINED" 73
THE RESPONSE TO SELECTION 74
Genes Affect the Physiological Bases of Behavior 77
GENES AND NERVOUS SYSTEMS 79
GENES AND GARTER SNAKE BEHAVIOR 81

4 The Development of Behavior 89

Development as a Gene–Environment Interaction 89
HORMONES AND THE DEVELOPMENT OF MATERNAL BEHAVIOR 94
THE DEVELOPMENT OF SINGING BEHAVIOR IN BIRDS 95
ENVIRONMENTAL INFLUENCES ON SONG LEARNING IN SPARROWS 96
ENVIRONMENTAL INFLUENCES ON SONG LEARNING IN COWBIRDS 102
Developmental Resilience and Behavior 105
DEVELOPMENT IS RELIABLE 106
BEHAVIORAL DEVELOPMENT IN ABNORMAL CONDITIONS 108
DEVELOPMENTAL HOMEOSTASIS AND HUMAN BEHAVIOR 111
THE ADAPTIVE VALUE OF DEVELOPMENTAL HOMEOSTASIS 113

5 Nerve Cells and Behavior 117

The Neural Basis of Behavior 117
HOW DO MOTHS EVADE BATS? 119
ACTION POTENTIALS AND INFORMATION 122
Stimulus Filtering And Behavior 126
STIMULUS FILTERING BY VERTEBRATES 128
SOUND PERCEPTION IN BATS 129
SELECTIVE PERCEPTION 132
SPECIALIZED VISUAL PERCEPTION 135
Mechanisms of Motor Control 139
CENTRAL PATTERN GENERATORS 143
Navigation 147
BACKUP ORIENTATION MECHANISMS 149
OLFACTORY NAVIGATION? 150

6 The Organization of Behavior 159

Organizing Behavior in the Short Term: Command Centers 159
NEURAL INHIBITION AND BEHAVIOR 161
Changing Priorities and Circadian Rhythms 164
EXPLORING CIRCADIAN MECHANISMS 166
LONGER CYCLES OF BEHAVIOR 169
CHANGING PRIORITIES IN A CHANGING SOCIAL ENVIRONMENT 169
CHANGING PRIORITIES IN RESPONSE TO A CHANGING INTERNAL ENVIRONMENT 171
Seasonal Changes and Annual Cycles 174
THE ROLE OF THE ENVIRONMENT 176
SOCIAL INFLUENCES ON THE ANNUAL CYCLE 179
ASSOCIATED AND DISSOCIATED REPRODUCTIVE PATTERNS 181

7 The Evolution of Behavior: Historical Pathways 191

History and Adaptation 191
THE ADAPTIVE VALUE OF HEADLESS COPULATION 193
Reconstructing the History of Complex Traits 194
A NEW HYPOTHESIS ON *ARCHAEOPTERYX* FLIGHT 196
THE HISTORY OF BIPEDALISM IN HUMANS 200
Reconstructing Evolutionary History: Comparing Living Species 203
THE HISTORY OF HOST PREFERENCES OF BROOD PARASITES 206
The Lessons of History 207
CONSTRAINTS ON EVOLUTIONARY CHANGE 209

8 The Evolution of Adaptations 215

Behavioral Adaptation 215
Testing Adaptationist Hypotheses 218
A STRONG TEST OF THE PREDATOR-DISTRACTION HYPOTHESIS 220
THE COMPARATIVE METHOD 221
A COST–BENEFIT APPROACH 227
Criticisms of the Adaptationist Approach, and a Reply 230
THE VALUE OF THE ADAPTATIONIST APPROACH 233
THE PREVALENCE OF ADAPTATION 235

9 The Evolution of Communication 241

The History and Adaptive Value of a Signal 241
AN ADAPTIVE SIGNAL? 244
Reconstructing the History of Communication Signals 247
THE ORIGINS OF RECEIVING SIGNALS 248
HONEYBEE DANCES 250
THE HISTORY OF THE DANCE DISPLAYS 255
The Adaptive Value of Communication Signals 257
YELLING RAVENS 257
THE COSTS AND BENEFITS OF SIGNALING 260
COPING WITH ILLEGITIMATE RECEIVERS 264
THE COSTS AND BENEFITS OF SIGNAL RECEIVING 267
DECEPTION AND THREAT DISPLAYS 271

10 Finding a Place to Live 279

Habitat Selection 279
NEST SITE SELECTION BY HONEYBEES 281
HABITAT PREFERENCES AND FITNESS 283
Dispersing from One Place to Another 284
THE INBREEDING AVOIDANCE HYPOTHESIS 285
THE MATE COMPETITION HYPOTHESIS 286
CHANGING BREEDING LOCATIONS OR STAYING PUT 288
Migration 290
THE COSTS OF MIGRATION 290
THE BENEFITS OF MIGRATION 293
THE MIGRATION OF THE MONARCH BUTTERFLY 294
THE COEXISTENCE OF ALTERNATIVE MIGRATORY TENDENCIES WITHIN SPECIES 296
Territoriality 299
TERRITORIALITY AND REPRODUCTIVE SUCCESS 300
TERRITORIALITY AND CALORIES 304
CONDITIONAL TERRITORIALITY 306
LONG-TERM EFFECTS OF TERRITORIALITY 308
HOW LARGE SHOULD A TERRITORY BE? 309
WHY DO TERRITORY HOLDERS ALMOST ALWAYS WIN? 312
THE RESOURCE-HOLDING POWER HYPOTHESIS 314
THE PAYOFF ASYMMETRY HYPOTHESIS 315

11 Adaptive Feeding Behavior 321

Locating Food 321
DETECTING PREY BY ATTENDING TO COMPANIONS 324
FINDING PREY BY DECEIVING VICTIMS INTO REVEALING THEIR LOCATION 326
Selecting What to Eat 329
OPTIMAL CLAM SELECTION BY NORTHWESTERN CROWS 333
OPTIMAL MUSSEL SELECTION BY OYSTERCATCHERS 334
CRITICISMS OF OPTIMALITY THEORY 336
OPTIMAL FORAGING WHEN PREDATORS ARE AROUND 337
OPTIMAL FORAGING WHEN COMPETITORS ARE AROUND 339
Capturing Prey 340
SOCIALITY AND THE CAPTURE OF LARGE PREY 340
OPTIMAL FORAGING: HOW MANY PREY TO CAPTURE PER TRIP? 345
Consuming Food 346
WHERE TO CONSUME CAPTURED FOODS 348
WHEN TO EAT DIRT 349

12 Coping with Predators Adaptively 353

Making Detection Less Likely 353
RESTING SITE SELECTION AND SURVIVAL 355
REMOVING TELLTALE EVIDENCE 357
Making an Attack Less Likely 357
WARNING COLORATION AND BEHAVIOR 359
BATESIAN MIMICRY 361
ASSOCIATING WITH A PROTECTED SPECIES 364
ADVERTISING UNPROFITABILITY 366
Making Capture Less Likely 368
VIGILANCE AND SOCIALITY 369
ALARM SIGNALS 372
THE SELFISH HERD 374
THE DILUTION EFFECT 376
RAPID ESCAPE FLIGHT 378
Making Consumption Less Likely 380
MISDIRECTING CONSUMERS 383
ATTRACTING COMPETING CONSUMERS 385
Monarch Butterfly Defense Systems 387

13 Male and Female Reproductive Tactics 395

The Evolution of Males and Females 395
PARENTAL INVESTMENT 397

Sexual Selection and Parental Investment 398
SEX ROLE REVERSALS AS A TEST OF THE THEORY OF SEX DIFFERENCES 404

Competition for Copulations 407
SOCIAL DOMINANCE AND FITNESS 408
ALTERNATIVE MATING BEHAVIORS 412
STRATEGIES OR TACTICS? 414
THREE STRATEGIES OF A MARINE ISOPOD 415
THREE TACTICS OF A SCORPIONFLY 418

Competition for Eggs to Fertilize 419
SPERM COMPETITION AND MATE GUARDING 421

Mate Choice by Females in Relation to Material Benefits from Males 424
MATE CHOICE AND NUPTIAL GIFTS 426
SPERMATOPHORES AS NUPTIAL GIFTS 427
MATE CHOICE AND ACCESS TO MONOPOLIZED RESOURCES 428
MATE CHOICE AND MALE PARENTAL CARE 429

Mate Choice by Females When Males Offer Sperm Alone 432
FEMALE PREFERENCES FOR EXTRAVAGANT TRAITS 434
TESTING THE GOOD GENES AND RUNAWAY SELECTION HYPOTHESES 436

14 The Ecology of Mating Systems 445

Diversity in Male Mating Systems 445
HYPOTHESES ON MONOGAMY BY MALES 446
MONOGAMY IN MAMMALS 447
MONOGAMY IN BIRDS 448
EXTRA-PAIR COPULATIONS IN "MONOGAMOUS" BIRDS 451
EXTRA-PAIR COPULATIONS FROM THE FEMALE'S PERSPECTIVE 452

Polyandry 456

The Varieties of Polygyny 459
FEMALE DEFENSE POLYGYNY: THE FEMALE PERSPECTIVE 463
RESOURCE DEFENSE POLYGYNY 464
RESOURCE DEFENSE POLYGYNY: THE FEMALE PERSPECTIVE 466
SCRAMBLE COMPETITION POLYGYNY 468
LEK POLYGYNY 470
WHY DO LEKS FORM WHERE THEY DO? 472
THE LEK PARADOX AND FEMALE CHOICE 473

The Mating Systems of the Dunnock 474

15 Caring For Offspring 481

Why is Parental Care More Often Provided by Females? 481
THE ORDER OF GAMETE RELEASE HYPOTHESIS 483
THE ASSOCIATION WITH YOUNG HYPOTHESIS 483
WHY ARE MALE FISHES SO OFTEN PATERNAL? 484
WHY ARE MALE BURYING BEETLES PATERNAL? 485

How to Maximize the Parental Payoff 487
OFFSPRING RECOGNITION: COMPARATIVE STUDIES 489
OFFSPRING RECOGNITION IN GULLS? 491
ADOPTION IN THE FATHEAD MINNOW 493
TOLERANCE OF SIBLICIDE: A PARENTAL PUZZLE 494

16 The Ecology of Social Behavior 501

The Costs and Benefits of Sociality 501

The Evolution of Helpful Behavior 506
ALTRUISM AND INDIRECT SELECTION 507
HAMILTON'S RULE 510
HELPERS AT THE NEST 513
ALARM CALLS AND INDIRECT SELECTION 517
MATING COOPERATION AMONG MALES 520
MANAKIN COALITIONS AND COOPERATIVE COURTSHIP 521
COALITIONS AMONG BABOONS 523

The Evolution of Eusocial Behavior 524
EUSOCIALITY AND INDIRECT SELECTION 528
TESTING THE INDIRECT SELECTION HYPOTHESIS FOR EUSOCIALITY 531
EUSOCIALITY AND DIRECT SELECTION 532
THE ECOLOGY OF EUSOCIALITY 535

17 An Evolutionary Approach to Human Behavior 541

The Adaptationist Approach to Human Behavior 541

The Sociobiology Controversy 542

A Strategy for Developing Sociobiological Hypotheses 546
ALTERNATIVE HYPOTHESES ON ADOPTION 547

Adaptive Decision-Making: Human Sexual Behavior 550
MALE COMPETITION FOR MATES 551
COERCIVE SEX 553
SPERM COMPETITION AND MATE GUARDING 555
FEMALE MATE CHOICE 558
MALE MATE CHOICE 561

Adaptive Decision-Making: Parental Care 564
HELPING CHILDREN MARRY: DOWRIES AND BRIDEWEALTH PAYMENTS 569

Glossary 575

Bibliography 580

Illustration Credits 613

Author Index 614

Subject Index 616

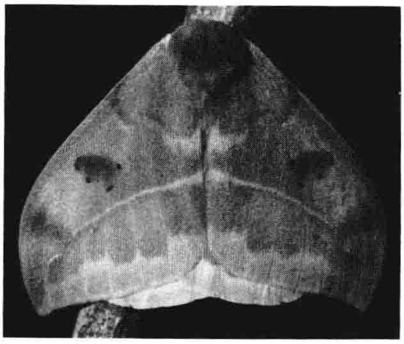
1

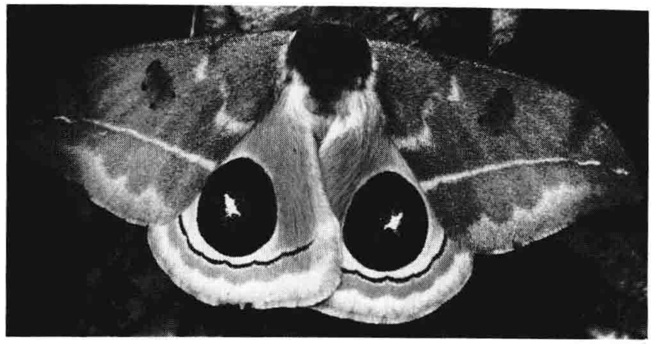
AN EVOLUTIONARY APPROACH TO ANIMAL BEHAVIOR

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 produced by the device attracted hundreds of moths on a good night, and many stayed on the sheet until morning, when I could inspect them at my convenience. Some mornings I found a huge bright yellow moth clinging to the sheet. This attractive moth, a member of the genus *Automeris,* held its forewings so that they covered its abdomen and hindwings. 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 large circular patches of blue, black, and white scales set on a deep yellow background. The patches looked like two eyes, which seemed to stare back at me (Figure 1).

Anyone seeing *Automeris* abruptly expose its hindwing "eyes" for the first time will surely wonder what is going on. I know I did. My questions about *Automeris* wing-flipping grew into a substantial list, but no matter how long the list, I could assign each question to one of just two categories:





1 *AUTOMERIS* MOTH FROM COSTA RICA. Left: Moth in its resting position with the forewings held over the hindwings. Photograph by the author. Right: After being jabbed in the thorax, members of this species pull the forewings forward to expose the "eyes" on the hindwings. Photograph by Michael Fogden.

"how questions," about the PROXIMATE CAUSES of the behavior, or "why questions," about its ULTIMATE CAUSES [619, 707]. How questions ask how an individual manages to carry out an activity; they ask how mechanisms *within* an animal operate, enabling the creature to behave in a certain way. Why questions ask *why* the animal has evolved the proximate mechanisms that cause it to perform an activity. The two kinds of questions are complementary, not antagonistic, because they deal with fundamentally different levels of analysis.

How Questions

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

What is the causal relationship between the animal's genes and its behavior?

Is the trait to some extent inherited from the moth's parents?

How has the development of the moth from a single cell to a multi-million-celled adult affected its behavior?

What stimuli trigger the response and how are these stimuli detected?

How are the animal's nervous and muscular systems integrated to enable it to react to a poke in the side?

What these five 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 its amazing hindwings. The diversity of proximate questions is great enough, however, that we can subdivide them into two complementary groups, one dealing with the effects of heredity and development on the construction of the mechanisms underlying wing-flipping, and the other dealing with how the fully developed mechanisms actually work to cause the reaction.

With respect to the influence of heredity on development, we can ask how the special touch receptors, brain cells, and muscle controllers used in the wing-flipping reaction arise in an individual. The adult moth began life as a fertilized egg, a single cell that contained genetic instructions donated by its father and mother. These instructions affected the development of the moth, channeling the proliferation and specialization of cells along certain pathways that produced a nervous system with special features in the adult insect. This is a wonderfully complex process, still poorly understood for any organism, let alone for *Automeris* moths.

Even if the development of the response were completely understood, we could still explore how the fully developed neural mechanisms within the adult moth detect certain kinds of stimulation and how messages are then relayed to activate a muscular response. Not a single person has examined the neurophysiological foundation of the behavior of the *Automeris* moth that I bothered in Monteverde, but the underlying mechanisms are there waiting for future investigations.

Why Questions

Let's say that you personally discovered everything there was to know about the genetic–developmental and sensory–motor causes of the wing-flipping behavior of *Automeris* moths. You could still continue to study the moth's behavior in order to satisfy your curiosity about a whole set of very different questions, such as:

What is the purpose, the function, of the behavior?

How does the behavior assist the individual in overcoming obstacles to survival and reproduction?

How has the behavior evolved and how has it changed over evolutionary time?

What was the original step in the historical process that led to the existence of the current behavior?

These are all questions about the evolutionary, or ultimate, reasons for why an animal does something. Why does the moth suddenly lift its forewings and expose its eye spots when it is molested? The British scientist David Blest suggested that the action became common because it protects the moth from predators, startling and frightening away moth-eating birds that mistake the eye spots for the eyes of *their* enemy, predatory owls [85].

If the result of wing-flipping behavior has been to save the lives of moths in the past, then the evolutionary process is partly responsible for the behavior of individuals today. The genes that exist in contemporary moths are a tiny subset of all the genes that have ever existed. Those that have managed to persist to the present are genes that have in some way contributed to their own survival. If a gene influenced the appearance or behavior of a moth in ways that helped the moth frighten away predatory birds, that gene would presumably have a better chance of being passed on to descendants of that moth. This process could help explain why

Automeris moths living in Monteverde have inherited genetic mechanisms that promote the development of wing-flipping behavior. The developmental plan, and therefore the behavioral abilities, of each member of the species alive today has been defined by differences in gene survival that occurred during the history of the species.

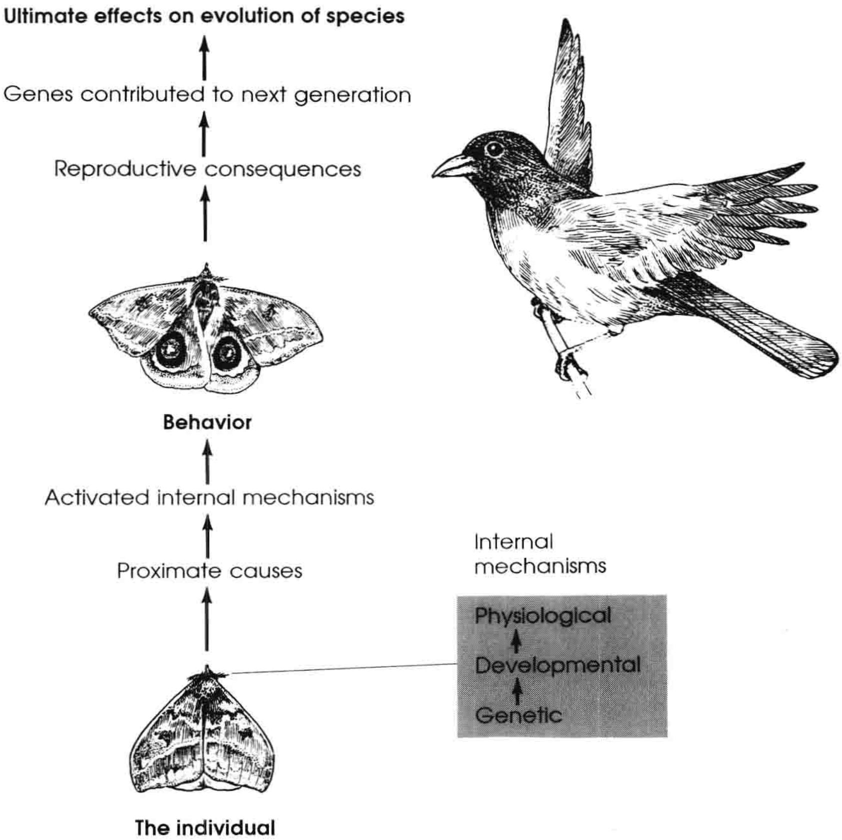
Thus, studying the current function of behavior can give us insight into the ultimate or evolutionary causes of behavior. But there is another component to the evolutionary analysis of behavior, and that has to do with how the trait came into being and then was (perhaps) modified over time until it reached its current state. The present sharp wing-flipping behavior was surely not always practiced by the ancestors of modern-day *Automeris*. Probably the initial phase involved certain wing movements associated with taking flight, movements that have been modified over time, just as the color pattern of the hindwings has certainly changed over time [84]. A full understanding of the ultimate causes of wing-flipping requires investigation into the initial form and subsequent alteration of the behavior over the millennia.

Table 1 summarizes this discussion about the two fundamental levels of analysis, proximate and ultimate, in the study of behavior. You should now be able to discriminate between mechanistic and evolutionary explanations. If someone were to make the claim that *Automeris* moths expose their hindwings when pecked because their nervous system controls the wing-flipping response, this is a proximate explanation—as are all hypotheses based on genetic, developmental, neural, or hormonal mechanisms found within the body of an individual. If someone were to propose that the action evolved because of past predation pressure on the species, you would know that this is an ultimate explanation—as are all explana-

TABLE 1 Levels of analysis in the study of animal behavior

PROXIMATE CAUSES
1 Genetic–developmental mechanisms
Effects of heredity on behavior
Genetic–environmental interactions during development that produce sensory–motor mechanisms
2 Sensory–motor mechanisms
Detection of environmental stimuli: Operation of nervous systems
Adjustment of internal responsiveness: Operation of hormonal systems
Carrying out responses: Operation of skeletal–muscular systems
ULTIMATE CAUSES
1 Historical pathways leading to a behavior
Origin of the behavior and its alteration over time
2 Past effects of natural selection in shaping a current behavior
Past and current utility of the behavior in reproductive terms

Sources: Holekamp and Sherman [454], Sherman [853], and Tinbergen [931].



2 PROXIMATE AND ULTIMATE CAUSES OF BEHAVIOR as illustrated by *Automeris* moth wing-flipping. At the proximate level, various mechanisms internal to an individual moth enable it to execute the behavior. At the ultimate level, the moth's response to potential predators affects its reproductive success as measured by the number of copies of its genes that are passed on to the next generation. The history of differential reproductive success among individuals determines what genes survive from generation to generation and therefore what genetic information is available to influence the development of moths in the current generation.

tions that deal with the reproductive or adaptive value of a trait and its historical basis, its evolutionary foundation (Figure 2).

Moreover, if someone were to claim that work on the genetic (or neural) mechanisms of the response made it unnecessary to examine hypotheses about the possible reproductive benefits of the response, you would know that they are mistaken; learning how mechanisms work does not answer questions about why these particular mechanisms exist. A full analysis of any behavior involves both proximate and ultimate explanations.