# Contents

#### PREFACE XVII



#### PRINCIPLES OF ANIMAL BEHAVIOR 2

Types of Questions and Levels of Analysis 5

Three Foundations 6

Foundation 1—Natural Selection 7
Foundation 2—Individual Learning 10
Foundation 3—Cultural Transmission 13

Conceptual, Theoretical, and Empirical Approaches 16

Conceptual Approaches 16 Theoretical Approaches 18 Empirical Approaches 20

An Overview of What Is to Follow 24

INTERVIEW WITH DR. E. O. WILSON 22



# THE EVOLUTION OF BEHAVIOR 26

**Artificial Selection 29** 

Natural Selection 31

Selective Advantage of a Trait 31 How Natural Selection Operates 33

**Behavioral Genetics 39** 

Mendel's Laws 39 Locating Genes for Polygenic Traits 41 Dissecting Behavioral Variation 42

#### The Modern Theoretical Framework for Animal Behavior 44

Sociobiology and Selfish Genes 44 Antipredator Behavior in Guppies 45

#### Adaptation 50

## Genetic Techniques to Test Hypotheses in Animal Behavior 53

Kinship and Naked Mole Rat Behavior 53 Coalition Formation 56

#### Phylogeny and the Study of Animal Behavior 58

Phylogenetic Trees 58
Phylogeny and Parental Care 62
Phylogeny, Mating Systems, and Male Aggression 64

INTERVIEW WITH DR. ALAN GRAFEN 66



#### PROXIMATE FACTORS 72

#### **Ultimate and Proximate Perspectives 75**

#### **Hormones and Proximate Causation 81**

The Long-Term Effects of In-Utero Exposure to Hormones 86 Stress Hormones and Spatial Memory in Rats 87

#### Neurobiological Underpinnings of Behavior 90

The Nervous Impulse 91
Neurobiology and Learning in Voles 93
Vocalizations in Plainfin Midshipman Fish 95
Sleep and Predation in Mallard Ducks 98

#### Molecular Genetics and Animal Behavior 100

Ultraviolet Vision in Birds 100
Song Acquisition in Birds 103

#### **Development and Animal Behavior 105**

Early Development and Its Effect on Parental Behavior in the Oldfield Mouse 105

Development, Temperature, and Ovipositing Behavior in Wasps 107

#### Foraging in Honeybees: An Integrated Proximate Analysis 108

Mushroom Bodies and Honeybee Foraging 109
Genes, mRNA, and Honeybee Foraging 110
Hormones and Honeybee Foraging 112

INTERVIEW WITH DR. GEOFFREY HILL 114



#### LEARNING 118

#### What Is Individual Learning? 121

#### **How Animals Learn 123**

Learning from a Single-Stimulus Experience 124 Pavlovian (Classical) Conditioning 125 Instrumental (Operant) Conditioning 130

#### Why Animals Learn 131

Within-Species Studies and the Evolution of Learning 131
Population Comparisons and the Evolution of Learning 135
A Model of the Evolution of Learning 138

#### What Animals Learn 140

Learning Where Home Is Located 140 Learning about Your Mate 142 Learning about Familial Relationships 143 Learning about Aggression 144

# Molecular Genetics and Endocrinology of Learning 146

Molecular Genetics of Learning in Rats 146 Endocrinology of Learning in Rats 147

# Phylogeny and the Neurobiology of Learning 149

INTERVIEW WITH DR. SARA SHETTLEWORTH 150



### **CULTURAL TRANSMISSION 156**

#### What Is Cultural Transmission? 162

What's So Important about Cultural Transmission? 163 Effects of Others on Behavior 164 Social Learning 167 Teaching in Animals 173

#### Modes of Cultural Transmission 176

Vertical Cultural Transmission 176 Horizontal Cultural Transmission 178 Oblique Cultural Transmission 178

# The Interaction of Genetic and Cultural Transmission 179

The Grants' Finches 180 Guppy Mate Choice 181

#### Cultural Transmission and Brain Size 182

INTERVIEW WITH DR. CECILIA HEYES 184



#### SEXUAL SELECTION 188

Intersexual and Intrasexual Selection 190

**Evolutionary Models of Mate Choice 193** 

Direct Benefits and Mate Choice 194
Good Genes and Mate Choice 196
Runaway Sexual Selection 204
Sensory Bias and the Emergence of Mate Choice 205

#### Learning and Mate Choice 208

Sexual Imprinting 209 Learning and Mate Choice in Japanese Quail 210

#### **Cultural Transmission and Mate Choice 211**

Mate-Choice Copying 212 Song Learning and Mate Choice in Cowbirds 214

#### Male-Male Competition and Sexual Selection 215

Red Deer Roars and Male-Male Competition 216
Male-Male Competition by Interference 217
Male-Male Competition by Cuckoldry 219

INTERVIEW WITH DR. ANNE HOUDE 222



#### MATING SYSTEMS 226

#### Different Mating Systems 228

Monogamous Mating Systems 229 Polygamous Mating Systems 232 Promiscuous Mating Systems 238

#### The Ecology and Evolution of Polygynous Mating Systems 241

Polygyny and Resources 241 The Polygyny Threshold Model 242 Extrapair Copulations 245 Sperm Competition 248

#### Multiple Mating Systems in a Single Population? 253

Dunnocks 254

INTERVIEW WITH DR. NICK DAVIES 256



#### KINSHIP 260

#### Kinship and Animal Behavior 263

#### Kinship Theory 264

Relatedness and Inclusive Fitness 266 Family Dynamics 269

#### Conflict within Families 280

Parent-Offspring Conflict 280
Sibling Rivalry 284

#### Kin Recognition 286

Matching Models 287
Rule-of-Thumb Models of Kin Recognition 289

INTERVIEW WITH DR. FRANCIS RATNIEKS 290



#### COOPERATION 294

#### The Range of Cooperative Behaviors 297

Helping in the Birthing Process 297 Social Grooming 298

#### Paths to Cooperation 300

Path 1: Reciprocity 300

Path 2: Byproduct Mutualism 313

Path 3: Group Selection 317

#### Coalitions 321

Coalitions in Baboons 322

Alliances and "Herding" Behavior in Cetaceans 323

#### Phylogeny and Cooperation 324

Phylogeny and Cooperative Breeding in Birds 324 Phylogeny and Cooperation in Social Spiders 325

#### Interspecific Mutualisms 326

Ants and Butterflies—Mutualism with Communication? 327

INTERVIEW WITH DR. HUDSON KERN REEVE 328



#### FORAGING 334

Finding Food and the Search Image 337

#### **Optimal Foraging Theory 338**

What to Eat 338
Where to Eat 343
Specific Nutrient Constraints 345
Risk-Sensitive Foraging 347

# Foraging and Group Life 350

Group Size 350 Groups, Public Information, and Foraging 352

#### Natural Selection, Phylogeny, and Seed Caching 353

Hippocampal Size and Caching Ability 354 Phylogeny and Caching Ability 355

#### Learning and Foraging 356

Foraging, Learning, and Brain Size in Birds 356 Planning for the Future 358 Social Learning and Foraging 360

INTERVIEW WITH DR. JOHN KREBS 364



#### **ANTIPREDATOR BEHAVIOR 368**

#### **Avoiding Predators 372**

Blending into the Environment 372 Being Quiet 373 Choosing Safe Habitats 376

#### What to Do When Prey Encounter Predators 377

Fleeing 378
Approaching Predators 382
Feigning Death 386
Signaling to Predators 388
Fighting Back 390

#### Predation and Foraging Trade-offs 393

INTERVIEW WITH DR. ANNE MAGURRAN 394



#### **COMMUNICATION 400**

#### Communication and Honesty 404

#### **Communication Solves Problems 406**

Problem: How to Coordinate Group Foraging 407
Problem: How to Find and Secure a Mate 414
Problem: How to Warn Others about Predators 419

INTERVIEW WITH DR. RUFUS JOHNSTONE 424



# HABITAT SELECTION, TERRITORIALITY, AND MIGRATION 430

#### Models of Habitat Choice 434

The Ideal Free Distribution Model and Habitat Choice 434 The IFD Model and Foraging Success 435

#### **Territoriality 437**

Territoriality and Learning 438
Territory Owners and Satellites 439
How to Keep a Territory in the Family 441
Conflict within Family Territories 442

# Migration 443

Migration and Navigation 444 The Heritability of Migratory Restlessness 449 Migration and Defense against Parasites 450 Phylogeny and Migratory Behavior 450

INTERVIEW WITH DR. JUDY STAMPS 452



# AGGRESSION 456

Fight or Flight? 460

#### Game Theory Models of Aggression 462

The Hawk-Dove Game 464
The War of Attrition Model 468
The Sequential Assessment Model 470

#### Winner, Loser, Bystander, and Audience Effects 472

Winner and Loser Effects 472
Bystander Effects 478
Audience Effects 482

INTERVIEW WITH DR. KAREN HOLLIS 480



#### **PLAY 486**

Defining Play 489

#### Types and Functions of Play 490

Object Play 490 Locomotor Play 495 Social Play 498 A General Theory for the Function of Play 503

# Endocrinological and Neurobiological Bases of Play 504

Play Fighting in Young Male Rodents 504
Basis of Sexual Play in Young Belding's Ground Squirrels 508

#### A Phylogenetic Approach to Play 508

INTERVIEW WITH DR. BERND HEINRICH 510



#### AGING AND DISEASE 514

Senescence in the Wild? 517

#### Theoretical and Empirical Perspectives on Senescence 518

The Antagonistic Pleiotropy Model 519
Disposable Soma Theory and Longevity 520

#### Hormones, Heat-Shock Proteins, and Aging 525

Glucocorticoids, Stress, and Aging 525 Heat-Shock Proteins and Aging 526

#### Disease and Animal Behavior 526

Avoidance of Disease-Filled Habitats 527 Avoidance of Diseased Individuals 528 Self-Medication 529 Why Some Like It Hot 532

INTERVIEW WITH DR. RICHARD WRANGHAM 534



# **ANIMAL PERSONALITIES 538**

#### **Boldness and Shyness 542**

Bold and Shy Pumpkinseeds 543 Guppies, Boldness, and Predator Inspection 545

#### Some Case Studies 547

Hyena Personalities 547
Octopus and Squid Personalities 548
Ruff Satellites 551
Natural Selection and Personality in Great Tit Birds 553
Chimpanzee Personalities and Cultural Transmission 554

#### Coping Styles 555

#### Some Practical Applications of Animal Personality Research 558

Predators and Domesticated Prey 558 Guide Dog Personalities 558

INTERVIEW WITH DR. JEROME KAGAN 560

GLOSSARY 565
REFERENCES 571

**CREDITS 621** 

INDEX 623