



EVOLUTION and ECOLOGY of the ORGANISM

Michael R. Rose

*Department of Ecology and Evolutionary Biology,
University of California, Irvine*

Laurence D. Mueller

*Department of Ecology and Evolutionary Biology,
University of California, Irvine*



Upper Saddle River, NJ 07458

Library of Congress Cataloging-in-Publication Data

Rose, Michael R.

Evolution and ecology of the organism / Michael R. Rose, Laurence D. Mueller.—1st ed.

p. cm.

Includes index.

ISBN 0-13-010404-3

1. Evolution (Biology) I. Mueller, Laurence D. II. Title.
 QH366.2.R67 2005 576.8—dc22 2004028588

Publisher: Sheri L. Snavely

Editor: Teresa Ryu Chung

Editor in Chief, Science: John Challice

Project Manager: Karen Horton

Senior Media Editor: Patrick Shriner

Production Editor: Debra A. Wechsler

Executive Managing Editor: Kathleen Schiaparelli

Assistant Managing Editor: Beth Sweeten

Development Editor: Anne Reid

Editor in Chief, Development: Carol Trueheart

Marketing Managers: Andrew Gilfillan, Shari Meffert

Manufacturing Buyer: Alan Fischer

Director of Marketing, Science: Linda Taft MacKinnon

Director of Creative Services: Paul Belfanti

Manager, Composition: Allyson Graesser

Desktop Administration: Joanne Del Ben

Electronic Page Makeup: Joanne Del Ben, Clara Bartunek,

Meg Montgomery

Creative Director: Carole Anson

Art Director: Jonathan Boylan

Interior Design: John Christiana

Managing Editor, Audio and Visual Assets: Patricia Burns

AV Production Manager: Ronda Whitson

AV Production Editor: Connie Long

Art Studio: Precision Graphics, Inc.

Copy Editor: Christianne Thillen

Director, Image Resource Center: Melinda Reo

Manager, Rights and Permissions: Zina Arabia

Interior Image Specialist: Beth Brenzel

Cover Image Specialist: Karen Sanatar

Image Permission Coordinator:

Photo Researcher: Sheila Norman

Editorial Assistant: Lisa Tarabokjia

Interior and Cover Design: Michael R. Rose and

Laurence D. Mueller

Cover illustration by Karina I. Helm



© 2006 Pearson Education, Inc.

Pearson Prentice Hall

Pearson Education, Inc.

Upper Saddle River, NJ 07458

All rights reserved. No part of this book may be reproduced in any form
 or by any means, without permission in writing from the publisher.

Pearson Prentice Hall™ is a trademark of Pearson Education, Inc.

Printed in the United States of America

10 9 8 7 6 5 4 3 2 1

ISBN 0-13-010404-3Pearson Education LTD., *London*Pearson Education Australia PTY, Limited, *Sydney*Pearson Education *Singapore*, Pte. Ltd.Pearson Education North Asia Ltd., *Hong Kong*Pearson Education Canada, Ltd., *Toronto*

Pearson Educación de México, S.A. de C.V.

Pearson Education—Japan, *Tokyo*Pearson Education *Malaysia*, Pte. Ltd.

*To the Mueller, Krieks, Parla, Horsey, Metal, and Rose Families,
Near and Far*

THE AUTHORS



MICHAEL R. ROSE

Michael Rose went to the University of Sussex in 1976 for doctoral studies with Brian Charlesworth on the fruit fly *Drosophila melanogaster*. There he began his work on the evolution of aging and created fruit flies with genetically postponed aging. In 1991, his book *Evolutionary Biology of Aging* appeared, offering a view of aging that was a complete departure from the views that had dominated the aging field since 1960. Rose received the Busse Research Prize from the World Congress of Gerontology. Among his other honors is a teaching award from the School of Biological Sciences at the University of California, Irvine. He has written popular articles for *Technology Review* and *Scientific American*, as well as a general-audience book, *Darwin's Spectre: Evolutionary Biology in the Modern World*. He has published a total of more than 200 scientific publications of all kinds. The 2004 book *Methuselah Flies* assembles selected articles from the last 25 years of work in the Rose laboratory. He is Professor of Ecology and Evolutionary Biology at the University of California, Irvine and the Director of the University of California Intercampus Research Program on Experimental Evolution.

LAURENCE D. MUELLER

Larry Mueller received his Ph.D. in 1979 from the University of California, Davis, where he studied under Francisco Ayala. Mueller then went on to do postdoctoral research in theoretical population genetics with Marcus Feldman at Stanford University. He was an Assistant and Associate Professor at the Washington State University before assuming his current position of Professor of Ecology and Evolutionary Biology at the University of California, Irvine. Mueller has published over 70 research papers in the fields of evolution, population genetics and population ecology. He is also the author of *Stability in Model Populations* with Amitabh Joshi. In his current research, Mueller uses experimental evolution to study problems like density-dependent natural selection and the evolution of late-life demographic patterns in *Drosophila*.

PREFACE

This book introduces biology students to the basic concepts of the spectrum of fields that we call Darwinian biology, a spectrum that includes population genetics, population ecology, community ecology, macroevolution, physiological ecology, systematics, and functional morphology. Charles Darwin first brought this type of science to fruition and all these fields owe their foundations to his pioneering work, directly or indirectly. Our primary goal in the book is to elicit the students' interest. Secondarily we want to prepare undergraduate students for more advanced specialist courses in Darwinian biology as they pursue their degrees. We have adopted the following means to achieve these ends:

- Evoking Darwinian theory using stepped-out equations and concrete graphics to foster quantitative intuition.
- Using examples illustratively rather than exhaustively, to support and sharpen the student's understanding.
- Using evocative text to give the student an appreciation for the drama of the science and the color of its material.
- Using a magazine format that allows text and graphics to combine synergistically, with close juxtaposition.
- Consistently emphasizing concepts over details and scientific reasoning over terminology.

We want to help students over the hump that keeps them from understanding state-of-the-art texts in evolution, ecology, physiology, and cognate fields. Our hope is that using this book will make students more interested in Darwinian science, and faculty more willing to teach it. For two decades biology curricula have been dominated by cell and molecular biology, with Darwinian biology relegated to passing mention in introductory courses or to small advanced courses taken by few students. This is ironic at a time when the abundance of sequence data from molecular biology pointedly confronts biology with its need for Darwinian theories and analytical tools. Yet that toolkit has mostly fallen into disuse, poorly understood even by many biology faculty. The time for the rediscovery of this other half of biology has arrived.

The general theme of the book is the interconnectedness of organism, environment, and evolution. In studying the book, students should develop an integrated understanding of the organism that is founded in evolution and ecology. Just as biochemistry and molecular biology provide the foundation for our understanding of the cell, we use evolutionary biology and ecology here to construct a foundation for understanding the organism.

With this in mind, *Evolution and Ecology of the Organism* (henceforth *EEO*) integrates the component Darwinian disciplines. Instead of three separate sections for Evolution, Ecology, and Organismal Biology, thematic interconnections have been developed that combine elements of all these areas throughout the text. In so doing, *EEO* follows the precedent of contemporary research, in which ecologists, for example, use molecular genetic data and phylogenetic analysis.

Level

One of the most important issues for any textbook is that of level. There are a number of excellent advanced textbooks in ecology, evolution, and organismal biology. They are not going to be displaced by *EEO*. Each of those books already approaches 1000 pages in length. In order to achieve a comparable scope and replace three of these advanced disciplinary books, *EEO* would then need to be 2200 pages long. As you can see, it is not such a weighty tome.

In addition, *EEO* does not compete with general biology texts, which introduce students to the diversity of life-forms, cells, and habitats. Such books are the factual starting point for biology degrees, and have only rudimentary introductions to the conceptual content and empirical results of evolutionary biology or ecology. *EEO* will be best comprehended and utilized by students who have already taken a good introductory biology course.

The content of *EEO* is primarily aimed at the biology major in the second or third year of the college or university curriculum. However, students who have taken AP biology can begin their university education with courses based on *EEO*. At the other end of the spectrum, graduate students, post-docs, and faculty from other areas of biology may find *EEO* a helpful source of

basic information about Darwinian biology as well. But these qualifications aside, we would expect *EEO* most often to be assigned to second and third year biological science majors as part of their core curriculum. Such text adoptions might be for courses called “Ecology, Evolution, and Organism” or “Integrative Biology.” Or it might be assigned in a sequence of courses called “Ecology,” “Evolutionary Biology,” etc. In the process of sending out the text for review and talking to our colleagues, we have heard of a number of variations on these themes.

A sensible question might be why don’t these courses just use the traditional advanced texts in combination? For exceptionally well-prepared students, this may be workable. However, our experience is that the vast majority of biology majors become alienated from the study of ecology and evolution by the narrow specialization and quantitative detail of advanced texts in our disciplines. While advanced students may already understand the interconnections between population ecology, behavioral ecology, and population genetics, for example, intermediate-level students need an integrative framework within which to place the findings of these particular disciplines. We supply such an integration of Darwinian biology in a way that multiple separate texts cannot.

Format

EEO breaks with tradition with respect to format as well as content, to meet its twin goals of communication and integration. In *EEO*, the concepts are the focus. Because of this, these concepts are rendered primarily in visual form. Biology research is now image-driven, meaning that most of our discussions are based on images and photographs that convey our ideas. The use of dramatic colorful illustrations is commonplace in biology seminars. *EEO* is put together with graphics and photographs as the foreground elements and detailed text content as a background element. We try to make Darwinian biology lively and appealing.

Because *EEO* assembles the material so that at least half of it is conveyed graphically—and we consider that half to be essential content—we have designed the book so that all the one- or two-page spreads are art-centered and self-contained. These spreads are designed to convey a single message. That single message is embodied by a single declarative sentence, displayed prominently at the top of the page. In this way, information is focused into distinct nuggets, which we call Modules.

We are excited about this book. It has been a very important project for us and we have devoted long hours

to its creation, looking forward to the day when students would sit down with the book and be enticed, we hope, by the fascinating world of Darwinian biology. We would appreciate any suggestions you might have about the book, how it works for you in your classroom, what additional content should be added, and so on. Please contact us at mrrose@uci.edu or ldmuelle@uci.edu and let us know what you think.

Acknowledgments

We are very grateful for the support and encouragement we have received from so many over the seven years we have been working on this book. The individuals who have directly contributed to this project are listed on the copyright page and in the acknowledgments list below. Still others contributed indirectly by supplying us with our formal and informal educations over the years, particularly our teachers, advisors, and colleagues, in many cases long before we actually started writing. Francisco J. Ayala, Brian Charlesworth, James F. Crow, Marcus W. Feldman, William D. Hamilton, Rudolf Harmsen, John Maynard Smith, and Sewall Wright have been our greatest direct influences. We know that we should have made greater use of the knowledge and the direction that we received from them, but time is running out on this edition of our book.

There are some individuals whom we would like to single out for particular thanks. Sheri Snively, our Publisher at Prentice Hall, has stayed with us throughout this project, from her immediate enthusiasm when we first broached the project to her in Larry’s office in 1997, to the last hectic days of New Year’s 2005, as everything was racing toward a conclusion. Her belief in our dream saw us through the days when we wondered if we were ever going to accomplish the goals we had set for *EEO*.

Paul Corey stood behind Sheri and us, providing wisdom and sagacity in his very natural way. Teresa Ryu Chung was our principal Prentice Hall editor for years and years, and indomitably put up with our vacillations and digressions. Erin Mulligan then took over to help us prepare our final draft. In getting the book to press, Production Editor Debra Wechsler has been unbelievable in her care, diligence, and determination; the book is as close to our vision as it is thanks to her. Carol Trueheart, Editor in Chief of ESM Development was there for us through this process with helpful doses of sanity. Development Editor Annie Reid and copy editor Chris Thillen made our words smooth and eloquent when we were all too bound up in circumlocution or confusion. Sheila Norman found amazing photographs, both ap-

appropriate and dramatic. The design team was led by Carole Anson. Art Director Jonathan Boylan directed the design, making so much of the book beautiful, at least in our eyes. Patricia Burns and Connie Long from Artworks created the art program, key to making the book such a visual feast. Lisa Tarabokja actually took our desperate phone messages, and Karen Horton scrambled to get us over the final finish line during the accuracy check.

We considered more than ten publishers for this project, and most of them would no doubt have been excellent, but we have found great fulfillment with Prentice Hall as a publishing partner. We have asked for a lot of help all the way through. What we have received has consistently exceeded our expectations, sometimes even our comprehension.

Our most important academic colleague on this project was George V. Lauder, who was originally slated to be an author. Unfortunately, he was called back to his natal stream at Harvard, which prevented him from

continuing with us. He contributed the first draft of Chapter 2 and was heavily involved in planning the content and format of the book.

Our departmental colleagues in Ecology and Evolutionary Biology, UC Irvine, have played a wide range of supportive roles in this project. At one point, we saw the book virtually as an embodiment of our Department's collective knowledge. But then we recovered our sanity, having realized that you couldn't write a reasonable textbook with ten or more authors. Other colleagues at the University of California as a whole also inspired us to keep going. Darwinian biology is somewhat like a big scary Scottish clan, with all the intellectual fistfights, theoretical afflatus, and drunken color that you might expect. But it is our home, and we love it.

Michael Rose and Larry Mueller,
Irvine, California

Reviewers

The authors would like to thank the colleagues who reviewed the manuscript for this book at various stages of the project.

William G. Ambrose, *Bates College*
Mary Ashley, *University of Illinois, Chicago*
Stewart Berlocher, *University of Illinois-Urbana*
Champaign
Robert Browne, *Wake Forest University*
Christina Burch, *University of North Carolina,*
Chapel Hill
John A. Cigliano, *Cedar Crest College*
Sarah Cunningham, *University of California, Berkeley*
Mark D. Decker, *University of Minnesota*
Paul W. Ewald, *University of Louisville*
Susan Fahrbach, *University of Illinois-Urbana*
Champaign
Scott Fay, *University of California, Berkeley*
Steve Frank, *University of California, Irvine*
Roberta J. Mason-Gamer, *University of Illinois, Chicago*
George Gilchrist, *College of William and Mary*
Katherine Goodrich, graduate student, *University of*
South Carolina

Mark Hafner, *Louisiana State University*
Gregory R. Handrigan, *Dalhousie University*
Allan Larson, *Washington University*
Andrea Lloyd, *Middlebury College*
Robert Marquis, *University of Missouri, St. Louis*
Michael McDarby, *Fulton-Montgomery Community*
College
Timothy A. Mousseau, *University of South Carolina*
Randolph Nesse, *University of Michigan*
Nicholas L. Rodenhouse, *Wellesley College*
Jay Rosenheim, *University of California, Davis*
Michael Ruse, *Florida State University*
Brody Sandel, *University of California, Berkeley*
Maria Servedio, *University of North Carolina,*
Chapel Hill
Diane Wagner, *University of Alaska, Fairbanks*

BRIEF CONTENTS

PART ONE INTRODUCTION TO DARWINIAN BIOLOGY 0

- Chapter 1 Darwin, Ecology, and Evolution 3
- Chapter 2 Evolutionary Trees in the Ecological Garden 43

PART TWO MACHINERY OF EVOLUTION 76

- Chapter 3 The Genetic Engine 79
- Chapter 4 Natural Selection 125
- Chapter 5 Molecular Evolution 165
- Chapter 6 Speciation and Extinction 187

PART THREE THE DARWINIAN ORGANISM 228

- Chapter 7 Life-History of the Organism 231
- Chapter 8 Physical Ecology of the Organism 255
- Chapter 9 Physiological Ecology: How Organisms Work 271
- Chapter 10 Balancing Birth and Death 297
- Chapter 11 Dispersal 329

PART FOUR ECOLOGY OF INTERACTING SPECIES 348

- Chapter 12 Competition 351
- Chapter 13 Predation 381
- Chapter 14 Parasitism and Mutualism 405
- Chapter 15 Communities & Ecosystems 437
- Chapter 16 The Biosphere and the Physical Environment 475
- Chapter 17 Conservation 507

PART FIVE DARWINIAN BIOLOGY IN EVERYDAY LIFE 528

- Chapter 18 Evolution and Ecology of Sex 531
- Chapter 19 Mating Strategies 557
- Chapter 20 Social Evolution 575
- Chapter 21 Human Evolution and Human Behavior 601
- Chapter 22 Darwinian Medicine 631

CONTENTS



PART ONE INTRODUCTION TO DARWINIAN BIOLOGY 0

Chapter 1 Darwin, Ecology, and Evolution 3

DARWIN'S LIFE 4

- 1.1 There are many Darwin myths, perhaps because Darwin had an impact on the general culture 4
- 1.2 Darwin grew up an intellectually curious, but unemployed, member of the English landed gentry 6

- 1.3 On the voyage of the *Beagle*, Darwin learned a lot of biology, but he did not discover evolution 8
- 1.4 Darwin intuited evolution from the differences between birds from the Galápagos Islands 10
- 1.5 Darwin developed the concept of natural selection to explain the direction of evolutionary change 12
- 1.6 Despite publishing the *Origin of Species*, Darwin was a much-honored scientist during his life 14

DARWIN'S ECOLOGY AND EVOLUTION 16

- 1.7 Darwin used ecology to create evolutionary biology 16
- 1.8 Malthus's essay led Darwin to apply ecology to other problems of evolutionary biology 18
- 1.9 Artificial selection allowed Darwin to develop the concept of evolution by natural selection further 19
- 1.10 To support his theory Darwin used the fossil record, but regarded it as highly imperfect 20

DARWIN NEEDED MENDEL 21

- 1.11 Evolution requires the inheritance of variation 21
- 1.12 Darwin tried to explain the mechanism of inheritance using his theory of pangenesis, but failed 22
- 1.13 Mendel solved the problem of inheritance, but it took time for Mendel's genetics to join with Darwinism 23

THE BIRTH OF MODERN ECOLOGY 24

- 1.14 Predator-prey cycles and the origins of theoretical ecology 24
- 1.15 The idea of competitive exclusion and the birth of experimental ecology 26
- 1.16 The controversy between density-dependent and density-independent population regulation 28

DARWIN'S VIEW OF LIFE 30

- 1.17 Darwin's theories broke with prevailing biological doctrines, which were theological and vitalist in their foundations 30
- 1.18 Darwin's evolution was materialistic, unlike some other evolutionary theories 31
- 1.19 Natural selection supplies direction to Darwin's evolution, but is not itself directed 32
- 1.20 Ecology and natural selection combine in Darwin's theory to produce inefficient and historically contingent evolution 34

- 1.21 Darwin argued that all order in the history of life was a result of evolution by natural selection 36
- 1.22 The Darwinian universe and the organisms within it undergo materially important change 38
- 1.23 Despite great need, it took a long time for biology to be transformed by the Darwinian revolution 40

Chapter 2 Evolutionary Trees in the Ecological Garden 43

THE TREE CONCEPT 44

- 2.1 The history of life could have followed a variety of patterns, including an absence of evolution 44
- 2.2 Lyell's system of life allowed many origins of species and many extinctions, but no evolution 46
- 2.3 The only figure in the *Origin of Species* was an evolutionary tree 47
- 2.4 Modern evolutionary trees represent species as growing, splitting, and truncated branches 48
- 2.5 Evolutionary trees are often built using maximum parsimony 50

SOME IMPORTANT TREES 52

- 2.6 The origin of life and the three domains 52
- 2.7 Eukaryotic life evolved from endosymbiosis 54
- 2.8 The trees of prokaryotic life 56
- 2.9 The trees of eukaryotic life 57

USING TREES TO STUDY EVOLUTION 58

- 2.10 The classification of species can be explained elegantly with Darwin's evolutionary tree concept 58
- 2.11 Fossil differentiation often follows tree patterns 60
- 2.12 Biogeographic patterns can be explained in terms of geology, migration, and evolutionary history 62
- 2.13 Developmental patterns can be explained using evolutionary trees 64

THE COMPARATIVE METHOD 66

- 2.14 The comparative method uses the pattern of adaptation among species and their environments to infer the evolutionary causes of particular adaptations 66
- 2.15 Evolutionary trees can be used to test hypotheses of adaptation objectively 68
- 2.16 Homology: When similar features among related species are inherited from their common ancestor 70
- 2.17 Homoplasy: Parallel patterns in evolution that are due to natural selection, not ancestry 72



PART TWO MACHINERY OF EVOLUTION 76

Chapter 3 The Genetic Engine 79

HOW GENETICS WORKS 80

- 3.1 Genetics is central to modern biology 80
- 3.2 Reproduction may transmit one or two copies of the hereditary information to the next generation 82
- 3.3 Sexual reproduction recombines chromosomes containing many discrete loci 84

GENES IN POPULATIONS 86

- 3.4 Genes specify phenotypes, then the phenotypes are selected, which changes gene frequencies 86
- 3.5 The evolutionary state of a population is defined by its genotype frequencies 88
- 3.6 With no selection, allele frequencies do not change in randomly mating large populations 89
- 3.7 When the alleles of different loci are combined randomly, they are in linkage equilibrium 90

QUANTITATIVE CHARACTERS 92

- 3.8 Quantitative characters have to be studied statistically 92
- 3.9 When environmental (E) and genetic (G) influences on a phenotype (P) are independent, $V_P = V_G + V_E$ 94
- 3.10 The genes that make up a genotype may determine the phenotype additively or nonadditively 96
- 3.11 The resemblance of relatives is determined by the ratio of the additive genetic variance to the phenotypic variance 98

SEX AND RECOMBINATION 100

- 3.12** Population genetics is like shuffling and dealing cards 100
- 3.13** With random mating, sex-chromosome genes that start out at different frequencies move toward the same frequency 102
- 3.14** Recombination progressively breaks up nonrandom associations of alleles among loci 104

INBREEDING 106

- 3.15** Inbreeding is a bad thing in normally outbreeding natural populations 106
- 3.16** The degree of inbreeding can be calculated from the probability that parents share alleles from a common ancestor 108
- 3.17** When relatives mate regularly, homozygotes increase in frequency while heterozygotes decrease in frequency 110
- 3.18** Inbreeding tends to reduce the variance of quantitative characters within inbred lines 112
- 3.19** Inbreeding tends to reduce the average value of beneficial characters 114
- 3.20** Inbreeding can arise from the subdivision of populations 116

GENETIC DRIFT 118

- 3.21** Genetics is like card games, and genetic drift is like a trip to Las Vegas 118
- 3.22** Populations can undergo evolutionary change from genetic drift alone 120
- 3.23** Genetic drift can lead to the loss or fixation of alleles 122

Chapter 4 Natural Selection 125**DARWIN AND NATURAL SELECTION 126**

- 4.1** Darwin did not expect to observe natural selection 126
- 4.2** Darwin's original theory of natural selection made nature, through the struggle for existence, the breeder or selector 128
- 4.3** The workings of selection are evident in the procedures of artificial selection 129
- 4.4** Multiple generations of artificial selection can change a character substantially 130

THE CYCLE OF NATURAL SELECTION 132

- 4.5** Natural selection will sometimes have more impact than artificial selection, sometimes less 132

- 4.6** Natural selection requires genetic variation for characters related to fitness 134
- 4.7** Natural selection changes the patterns of survival and reproduction of organisms undergoing selection 135
- 4.8** With selectable genetic variation, natural selection changes the gene frequencies and phenotypes of the next generation 136

PHENOTYPIC PATTERNS OF NATURAL SELECTION 138

- 4.9** Natural selection acts powerfully on just a few characters at a time 138
- 4.10** Directional selection favors organisms with phenotypes that are at one extreme relative to the average phenotype 140
- 4.11** Stabilizing selection favors organisms that have intermediate characteristics 141
- 4.12** Disruptive selection favors organisms that have character values at both extremes of the phenotypic distribution 142

GENETIC MECHANISMS OF NATURAL SELECTION 144

- 4.13** Genetics complicates the action of natural selection 144
- 4.14** Selection in asexual populations increases mean fitness until the genetic variance in fitness is used up 146
- 4.15** When heterozygotes are intermediate, selection with sex is similar to selection without sex 147
- 4.16** Selection with recurring mutation prevents the achievement of maximum fitness 148
- 4.17** When heterozygotes are superior, selection maintains genetic variation 150
- 4.18** Selection in favor of rare genotypes can also maintain genetic variability 151

NATURAL SELECTION IN THE LABORATORY 152

- 4.19** Natural selection in the laboratory offers a view of what is possible in evolution 152
- 4.20** Bacterial evolution in the laboratory shows that the response to selection is very powerful at first, but tends to slow down 154
- 4.21** Laboratory experiments show that sexual populations can respond quickly to intense directional selection 156

NATURAL SELECTION IN THE WILD 158

- 4.22** The evolution of antibiotics illustrates the basic principles of natural selection in the wild 158
- 4.23** The best documented example of long-term natural selection in the wild is industrial melanism 160
- 4.24** Selection for increased beak size occurred in Darwin's finches on the Galápagos Islands 161

- 4.25** Human sickle-cell anemia is maintained by heterozygote superiority 162

Chapter 5 Molecular Evolution 165

GENES AND GENOMES 166

- 5.1** The genome is not a huge library of information 166
- 5.2** The eukaryotic gene is a complex structure with many nucleotides that do not code for amino acids 168
- 5.3** Transposable elements are mobile genes that make copies of themselves to move about the genome 170
- 5.4** Tandem arrays of genes increase and decrease gene number by unequal crossing over 172
- 5.5** Prokaryotic genomes are concatenations of genes with occasional inserted sequences, while eukaryotic genomes have large intergenic regions that play no apparent role in gene replication or function 173

NEUTRAL MOLECULAR EVOLUTION 174

- 5.6** The neutral theory of molecular evolution is based on genetic drift 174
- 5.7** The molecular clock is based on the observation that the rate of molecular evolution is roughly constant 176
- 5.8** Unlike nonsynonymous substitutions, synonymous substitutions proceed at a fairly uniform rate across a wide range of DNA sequences 178

SELECTIVE MOLECULAR EVOLUTION 180

- 5.9** Natural selection eliminates, substitutes, and maintains specific molecular genetic variants 180
- 5.10** It is uncertain how much nucleotide evolution is due to selection, but there is some evidence for selection on particular nucleotides 181
- 5.11** Genes that have been duplicated by reverse transcription may degenerate or evolve new functions 182
- 5.12** Genome size is highly variable, perhaps due to the proliferation of useless elements 184

Chapter 6 Speciation and Extinction 187

ALLOPATRIC SPECIATION 188

- 6.1** The biological species concept is based on the reproductive isolation of organisms that are given the opportunity to mate 188

- 6.2** Species may be isolated by a failure to reproduce that occurs after fertilization, which will select for isolation before fertilization 190
- 6.3** Geographical separation of populations fosters speciation 192
- 6.4** The genetic mechanisms of allopatric speciation may be adaptive or nonadaptive 194

SYMPATRIC SPECIATION 196

- 6.5** Sympatric speciation is difficult because of a lack of evolutionary isolation among groups 196
- 6.6** Polyploidization can produce instant sympatric speciation 198
- 6.7** Host-plant differentiation might cause sympatric speciation 200
- 6.8** Laboratory experiments show the feasibility of host-plant sympatric speciation 202

HYBRIDIZATION 204

- 6.9** Hybridization sometimes occurs in nature 204
- 6.10** Hybridization can produce polyploidization and instant speciation 206

SPECIES RADIATIONS 208

- 6.11** The Cambrian explosion was a spectacular radiation of animal species 208
- 6.12** The colonization of the Galápagos Archipelago by finches led to an adaptive radiation 210

PUNCTUATED EQUILIBRIUM 212

- 6.13** Mayr's speciation model implies punctuated equilibrium 212
- 6.14** Hopeful monsters can escape evolutionary stasis, in theory 214

RETAIL EXTINCTION 216

- 6.15** Extinctions destroy unique products of biological evolution 216
- 6.16** Normal biotic diversity is the result of a balance between the processes of speciation and extinction 218
- 6.17** Species that escape extinction tend to disperse widely over large geographic ranges 220

MASS EXTINCTION 222

- 6.18** Mass extinctions have intermittently eliminated a large proportion of living species 222
- 6.19** The mass extinctions probably arose from large-body impacts 224



PART THREE THE DARWINIAN ORGANISM 228

Chapter 7 Life History of the Organism 231

FITNESS AND LIFE HISTORIES 232

- 7.1 There are many types of life history 232
- 7.2 The fitness of semelparous organisms is the product of viability and fecundity 234
- 7.3 Iteroparous organisms have age-structured life histories 235
- 7.4 Populations with age structure can grow exponentially according to a stable age-distribution 236
- 7.5 In iteroparous organisms, fitness can be calculated from estimates of population growth rates 238
- 7.6 A small increase in semelparous fecundity may be favored over iteroparity 240

TRADE-OFFS IN LIFE-HISTORY EVOLUTION 241

- 7.7 When evolution increases one life-history character, another life-history character may decrease 241
- 7.8 Trade-offs between survival and reproduction may lead to the evolution of reproductive restraint 242
- 7.9 Trade-offs between offspring size and offspring survival lead to the evolution of intermediate size 244

EVOLUTION OF AGING 246

- 7.10 Aging has been studied from very different perspectives, including evolutionary biology 246

- 7.11 The survival and fertility of iteroparous plants and animals change with age 248
- 7.12 The force of natural selection acting on survival falls with adult age 250
- 7.13 Aging should not evolve in fissile organisms, but it should in life cycles without vegetative reproduction 251
- 7.14 Changing the force of natural selection can produce rapid evolution of aging patterns 252

Chapter 8 Physical Ecology of the Organism 255

TEMPERATURE AND LIGHT 256

- 8.1 Animals regulate their temperature in a variety of ways 256
- 8.2 Temperature profoundly influences organismal function 257
- 8.3 The temperature coefficient, Q_{10} , is used to express the effect of temperature on organismal function 258
- 8.4 Life at extreme temperatures reveals how organisms adapt to environmental stress 260
- 8.5 The physical properties of light striking the Earth constitute a key environmental factor mediating the physiology, distribution, and abundance of organisms 262

THE SIZE AND SHAPE OF ORGANISMS 264

- 8.6 The surface area to volume ratio of an organism affects its interaction with the environment 264
- 8.7 Changes in size have a major effect on organismal structure and function 266
- 8.8 Allometric methods are used to quantify changes in form and function associated with size 268

Chapter 9 How Organisms Work 271

CHEMICAL TRANSPORT 272

- 9.1 Whole organisms must cope with regulating solutes, gases, and water 272
- 9.2 Mechanisms of osmoregulation vary with environment due to distinct physical properties of air and water 273
- 9.3 Countercurrent exchange is used to control gas, heat, and ion flux 274
- 9.4 The uptake of oxygen by animals is accomplished by gills, lungs, and occasionally skin 276

- 9.5 Transport of water in plants uses transpiration and the physical properties of water 278
- 9.6 Animals transport fluids using specialized circulatory systems 280

EVOLUTION OF PHYSIOLOGICAL SYSTEMS 282

- 9.7 Desiccation is a major problem for terrestrial life 282
- 9.8 The ability to tolerate nitrogen wastes is molded by natural selection 284
- 9.9 Fat is beautiful when episodes of starvation are a predictable part of life 286

ENERGY PRODUCTION AND UTILIZATION 288

- 9.10 Many factors affect energy production and utilization 288
- 9.11 Metabolic rates are determined by a variety of factors 290
- 9.12 The “cost of transport” is a key metric of the energetic expense of moving in motile organisms 292
- 9.13 Energy is the basis of trade-offs for the evolution of many traits 294

Chapter 10 Balancing Birth and Death 297

THE POPULATION BOMB 298

- 10.1 Populations are collections of interbreeding individuals and the basic units of ecology and evolution 298
- 10.2 Populations may grow exponentially for short periods of time 300
- 10.3 In crowded populations, survival and fertility decline 302
- 10.4 Space is the important limiting resource for some populations 304

MALTHUSIAN SPECTERS 304

- 10.5 Experimental and theoretical ecology begin with investigations of single-species population growth 304
- 10.6 Density-regulated populations do not grow without bound 306
- 10.7 Density-regulated populations may exhibit chaotic behavior 308
- 10.8 Many organisms have complex life cycles that are density-regulated 310

DENSITY-DEPENDENT NATURAL SELECTION 312

- 10.9 The early theories of *r*- and *K*-selection were verbal 312

- 10.10 Great differences exist within species in their ability to tolerate crowding 314
- 10.11 Natural selection will increase rates of population growth 315
- 10.12 Natural selection often cannot increase population growth rates at high and low density simultaneously 316
- 10.13 The stability of populations is affected by the environment, but not selection 318

THE BOMB DIDN'T BLOW 320

- 10.14 A combination of increased food production and changes in demographic patterns have helped humans avert Malthusian catastrophes 320
- 10.15 Forecasting trends in human populations relies on knowledge of human birth and death patterns 322
- 10.16 The use of selection and genetic engineering vastly expanded agricultural productivity—though their long-term ecological effects are not known 324
- 10.17 Humans began to restrict their reproduction 326

Chapter 11 Dispersal 329

DISPERSAL AND MIGRATION 330

- 11.1 Migration and dispersal have a variety of important genetic and ecological consequences 330
- 11.2 A population may consist of many small populations linked by migration 332
- 11.3 Home-range size is related to energetic requirements 333
- 11.4 The dispersal of many marine organisms is mediated by ocean currents 334
- 11.5 Plant morphology affects the efficiency of passive dispersal 336

DORMANCY 337

- 11.6 Some species escape bad conditions by “travelling” through time: dormancy 337
- 11.7 Plant seeds are some of the longest-lasting dormant life-cycle stages 338
- 11.8 Many animals and plants survive in seasonal climates through the use of dormancy 340
- 11.9 Many organisms have neither long-term nor seasonal dormancy, but show intermittent dormancy 341

CONSEQUENCES OF DISPERSAL 342

- 11.10 Novel ecological structures: metapopulations 342
- 11.11 Connecting the genetics of populations: gene flow 344



PART FOUR ECOLOGY OF INTERACTING SPECIES 348

Chapter 12 Competition 351

THE ECOLOGICAL AND EVOLUTIONARY PROCESS OF COMPETITION 352

- 12.1 Plants and animals compete for resources 352
- 12.2 Competition for resources between individuals affects fitness 354
- 12.3 Plant competition for limited resources may lead to stable coexistence 356
- 12.4 Belowground plant structures compete for microorganisms, water, and essential nutrients 358
- 12.5 Intraspecific competitive ability responds to natural selection 360

THE CONSEQUENCES OF COMPETITION 362

- 12.6 Gause developed his competitive exclusion principle from experiments with *Paramecium* 362
- 12.7 Interspecific competition affects population dynamics 364
- 12.8 The Lotka-Volterra model of competition predicts competitive exclusion or stable coexistence 366
- 12.9 Competition affects the distribution of species 368

THE ECOLOGICAL NICHE 370

- 12.10 Several ecologists contributed to the development of the ecological niche concept 370
- 12.11 Determination of the realized niche can reveal how different species avoid competition 372

- 12.12 The number of species that exist in a particular environment may be determined by competition 374
- 12.13 Important morphological or behavioral traits may evolve, reducing levels of competition between species in a process called character displacement 376

Chapter 13 Predation 381

PREDATOR-PREY DYNAMICS 382

- 13.1 The dynamics of predator-prey populations are intimately connected 382
- 13.2 The Lotka-Volterra model of predator-prey dynamics predicts cycles, although for reasons which probably do not apply to natural populations 384
- 13.3 More realistic models incorporate density-dependent prey dynamics and predator satiation 386

HOW TO BE A PREDATOR 388

- 13.4 A variety of factors determine how predators forage 388
- 13.5 Foragers may optimize energy gain per unit of time, or minimize time spent foraging 390
- 13.6 The behavior of foraging animals often conforms to simple predictions 391
- 13.7 Central-place foragers should recover more food the farther they travel 392

HOW TO AVOID BECOMING PREY 394

- 13.8 The process of prey capture can be broken down into many stages 394
- 13.9 Prey may avoid predators by being difficult to find 396
- 13.10 Prey may avoid predators by looking like other distasteful species 397

PLANT-HERBIVORE INTERACTIONS 398

- 13.11 Plants show immediate and long-term reactions to herbivory 398
- 13.12 Herbivores employ various strategies to overcome plant defenses 400

Chapter 14 Parasitism and Mutualism 405

PARASITE-HOST INTERACTIONS 406

- 14.1 The specialized life cycle of parasites makes them useful for controlling certain pest species 406
- 14.2 Parasitoids cannot be too effective at finding hosts if they are to avoid extinction 408

- 14.3** Parasites are often very specialized in their feeding habits and life cycles, to match their hosts 410
- 14.4** As hosts evolve genetic resistance to parasites, the parasites evolve means of overcoming this resistance 412
- 14.5** The coevolution of hosts and parasites also depends on ecological factors 414

MUTUALISTIC INTERACTIONS 416

- 14.6** Mutualisms may provide several benefits to participating species, including nutrition, protection, and transportation 416
- 14.7** Mutualisms may involve the reciprocal exchange of essential nutrients 418
- 14.8** Mutualisms may involve the transportation of individuals or gametes 420
- 14.9** Mutualism may involve the provision of protection from predators or competitors 422
- 14.10** Mutualisms often evolve as a direct consequence of negative interactions between two or more species 424
- 14.11** The evolution of mutualisms should be facilitated when the reproduction of host and symbiont coincides 426
- 14.12** Levels of antagonism between hosts and parasites may depend on the frequency of opportunities for horizontal transfer 428

THE COEVOLUTIONARY PROCESS 430

- 14.13** Coevolution is a complex process that may depend on selection, migration, and genetic drift 430
- 14.14** Host-parasite phylogenies reveal common histories of speciation 432
- 14.15** Coevolution of bacteria and eukaryotic hosts shows little switching between pathogenic and mutualistic lifestyles 434

Chapter 15 Communities and Ecosystems 437

ENERGY FLOW 438

- 15.1** The flow of energy is a central organizing theme in community ecology 438
- 15.2** In most biological communities, all energy comes from the sun 440
- 15.3** The efficiency of energy transfer from one trophic level to the next varies among communities 442

EQUILIBRIUM AND NONEQUILIBRIUM COMMUNITIES 444

- 15.4** Community stability can be disrupted by sudden changes in the physical environment 444
- 15.5** The diversity of species in a community may depend on environmental disturbance 446
- 15.6** The number of species on islands represents a balance between extinction and immigration 447
- 15.7** Habitats go through predictable changes in species composition over time 448

COMMUNITY ORGANIZATION 450

- 15.8** The diversity of a community may be affected by competition, predation, or primary productivity 450
- 15.9** The number of species in a community may depend on predation 452
- 15.10** River communities show a top-down structure 454
- 15.11** Many features of food webs can be described by the cascade model 456
- 15.12** Food-web chain length is proportional to ecosystem size in lakes 458
- 15.13** Increased productivity can increase food-chain length but decrease stability 460
- 15.14** The structure of communities is also affected by the genetic structure of its members 462

ECOSYSTEMS 464

- 15.15** An important feature of ecosystems and their biological communities is their interaction with the physical environment 464
- 15.16** Essential nutrients are recycled through biological systems 466
- 15.17** Soil carbon levels are affected by temperature 468
- 15.18** Species diversity affects ecosystem performance 470

Chapter 16 The Biosphere and the Physical Environment 475

GLOBAL CLIMATES 476

- 16.1** Global climates are not static, but show major cycles every 100,000 years 476
- 16.2** The sun's energy and air currents are responsible for rain forests and deserts 478
- 16.3** The tilt of the Earth on its axis results in seasonal cycles in temperature and daylight 480
- 16.4** The ocean currents modify land climates 482
- 16.5** Atmospheric CO₂ and water vapor trap much of the sun's energy by a process called the greenhouse effect 484

LOCAL CLIMATES 486

- 16.6** Many factors may affect local climates 486
- 16.7** Local topography may affect climate: Rain-shadow deserts 488
- 16.8** The biological community may affect the climate 490

THE ECOLOGY AND EVOLUTION OF BIOMES 492

- 16.10** The ocean biomes cover 70 percent of the Earth's surface 492
- 16.11** The physical properties of water have important consequences for life in freshwater lakes and ponds 494
- 16.12** Adaptations to reduce water loss characterize the plant and animal life found in deserts 496
- 16.13** Forests are important terrestrial biomes often characterized by their dominant tree species 498

GLOBAL CHANGE 500

- 16.14** Human activities can quickly cause global environmental change 500
- 16.15** Human activities add gases to our atmosphere, leading to acid rain and ozone depletion 502
- 16.16** Human agricultural practices have increased the spread of deserts 504

Chapter 17 Conservation 507**BASICS OF CONSERVATION 508**

- 17.1** Conservation biology requires an understanding of the genetics, ecology, and physiology of managed populations 508
- 17.2** Ecological principles can be used to design reserves 510
- 17.3** The loss of habitat and habitat fragmentation leads to species extinctions 512
- 17.4** The last century has been marked by the loss of terrestrial forests and the acceleration of species extinctions 514
- 17.5** Ecological theory can be used to guide harvesting from natural populations 516
- 17.6** Risk assessment 518

APPLICATIONS 520

- 17.7** Application of conservation biology include designing reserves, reducing species extinctions, and managing exotic populations 520
- 17.8** Human activity has led to the extinction of many species in recent history 522
- 17.9** Some of the most prominent endangered species live in terrestrial ecosystems 524
- 17.10** Introduced exotic species often require management 526



PART FIVE DARWINIAN BIOLOGY IN EVERYDAY LIFE 528

Chapter 18 Evolution and Ecology of Sex 531

WHY IS SEX A PROBLEM? 532

- 18.1** Many species do not have sex 532
- 18.2** There is a two-fold fitness cost to producing sons 534
- 18.3** Sex requires sexual anatomy and exposure to predators or venereal diseases 536
- 18.4** Sex breaks up successful genotypes 537

IS SEX A GOOD THING DESPITE ITS PROBLEMS? 538

- 18.5** Sex cannot be explained by evolutionary history 538
- 18.6** With moderately frequent beneficial mutations, sex can speed up the rate of adaptation 540
- 18.7** Sex may reduce competition between siblings, increasing the fitness of sexual parents 542
- 18.8** Sex may generate variability required for hosts to evolve faster than their diseases and parasites 544
- 18.9** Sex may help get rid of deleterious mutations over the entire genome 546
- 18.10** Sex may be maintained because newly asexual females have depressed fitness 548

ORIGIN OF SEX 550

- 18.11** The origin of sex is even more complicated than its maintenance 550
- 18.12** Simple forms of sex can originate from mobile genetic elements 552
- 18.13** Recombination may have evolved as a by-product of selection for DNA repair 554

Chapter 19 Mating Strategies 557

GAMETES AND SEXES 558

- 19.1** Most sexual species have two types of gamete: Sperm and eggs 558
- 19.2** Unbiased sex ratios are normally favored by natural selection 559
- 19.3** The hymenopteran sex ratio system is often used to bias sex ratios when mating is incestuous 560

WHICH SEX SHOULD YOU BE? 561

- 19.4** Separate sexes evolve when it is hard to combine male and female sexual functions 561
- 19.5** The evolution of hermaphrodites also depends on the genetics of self-fertilization and the reproductive ecology of mating 562
- 19.6** Male and female roles can be reversed 564
- 19.7** Some species switch from one sex to another in order to increase fertility 566

HOW MANY PARTNERS? 568

- 19.8** There are three main mating patterns: Promiscuous, monogamous, and polygamous 568
- 19.9** Sexual selection favors individuals that are sexually attractive, combative, or territorial 570
- 19.10** The incubator is selected to find sexually attractive and helpful mates 572

Chapter 20 Social Evolution 575

GROUP SELECTION 576

- 20.1** Biological altruism is critical for social evolution 576
- 20.2** Group selection can prevail over individual selection 577
- 20.3** Group selection may be the best explanation for some cases of biological altruism 580

KIN SELECTION 582

- 20.4** Selection can act on families 582
- 20.5** Altruism toward relatives is favored when the cost is less than the benefit times relatedness 584

- 20.6** Insects with closely related sisters evolve complex social systems dominated by females 585
- 20.7** Kin selection led to the evolution of the burrowing societies of termites and naked mole rats 586

EVOLUTIONARY GAMES 588

- 20.8** Animals balance aggression and peaceful behavior as if social interaction were a game 588
- 20.9** Fitness depends on strategies that specify an animal's behavior in its conflicts 590
- 20.10** Violent behavior is rare if the costs of injury are greater than the benefits of victory 592
- 20.11** Natural selection may favor the Retaliator strategy, which is peaceful unless attacked 594
- 20.12** Bourgeois settles conflict using ownership 596

Chapter 21 Human Evolution and Human Behavior 601

THE HOMINID PHYLOGENY 602

- 21.1** Humans evolved from Old World Apes, which split from the rest of the primates 20 million years ago 602
- 21.2** Chimpanzees are our closest living relatives, followed by gorillas 604
- 21.3** There were at least two major upright hominid lineages, which may have included multiple species each 606
- 21.4** Upright human evolution featured expansion of the braincase, reduction in the jaws, and changes to the rest of the skeleton 608

HUMAN POPULATION GENETICS 609

- 21.5** Molecular genetic tools are crucial to unraveling the patterns of human evolution 609
- 21.6** Genetic evidence suggests that the Neanderthals belonged to a different species from the lineage that was ancestral to modern humans 610
- 21.7** There are two main theories concerning the ancestry of modern human populations 612
- 21.8** The latest data strongly support recent African proliferation of modern humans 614
- 21.9** Modern human populations seem to be a patchwork of local differentiation, with little racial differentiation 616

WHY DID EVOLUTION PRODUCE HUMANS? 618

- 21.10** The puzzle of our evolution has generated both intellectual aversion and gratuitous speculation 618

- 21.11** Humans must have evolved by intense directional selection for abilities derived from increased brain sizes 619
- 21.12** The hypothesis that we were selected only to use technology is undermined by the material simplicity of some cultures relative to their social complexity 620
- 21.13** The hypothesis that we were selected only for social calculation is undermined by our facility with complex material technologies 622
- 21.14** Human evolution probably involved a combination of selection pressures favoring both technology and social behavior 623

HUMAN BEHAVIOR FROM AN EVOLUTIONARY PERSPECTIVE 624

- 21.15** There is a long tradition of Darwinian analysis of human behavior, despite controversy about it 624
- 21.16** Some human behavior can be analyzed by the same methods used to study animal behavior 626
- 21.17** Human behavior may be organized to Darwinian ends without genetic specification, perhaps unconsciously 627

Chapter 22 Darwinian Medicine 631

HUMAN IMPERFECTION 632

- 22.1** Some of our medical problems arise from our evolutionary history 632
- 22.2** Genetic diseases are extreme forms of human imperfection generated by rare genotypes 634
- 22.3** From an evolutionary perspective, germline engineering has significant technological limitations 636
- 22.4** Somatic engineering is less problematic than germline engineering 638

CONTAGIOUS DISEASE 640

- 22.5** Human diseases are shaped by long-term evolution and global ecology 640

- 22.6** Some of our body's responses to contagious disease are beneficial: Vomiting is good for you 642
- 22.7** The evolution of pathogen virulence depends on the ecology of infection 644
- 22.8** Resistance to antibiotics has evolved in bacteria, requiring the development of new antibiotics 646
- 22.9** HIV illustrates the importance of rapid virus evolution in medicine 648

AGING 650

- 22.10** Evolution and genetics offer new hope for the medical treatment of the elderly 650
- 22.11** Humans live so long due to patterns of selection 652
- 22.12** Postponement of human aging will be achieved by combining evolutionary and other biotechnologies 654

BRAIN DISORDERS 655

- 22.13** Not all "mental illness" is pathological 655
- 22.14** Schizophrenia is an example of a Darwinian brain disorder 656
- 22.15** It is unclear whether all affect disorders are actively sustained by natural selection 658
- 22.16** The sociopath combines subjective well-being with pathological Darwinian outcomes 660

STATISTICAL APPENDICES 663

- APPENDIX A** Random variables and the rules of probability 663
- APPENDIX B** Statistical distributions and correlation 665
- APPENDIX C** Linear regression and the analysis of variance 667

GLOSSARY 669

BIBLIOGRAPHY 677

PHOTO CREDITS 681

INDEX 685

EVOLUTION and ECOLOGY of the ORGANISM

